University of Alberta

The Influence of Seed Dynamics on the Restoration Potential of White Box (*Eucalyptus albens* Benth.) Woodlands in Eastern Australia

By

David Irelan Board

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

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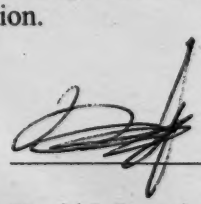

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "The Influence of Seed Dynamics on the Restoration Potential of White Box (*Eucalyptus albens* Benth.) Woodlands in Eastern Australia" submitted by David Irelan Board in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology

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Abstract

Efforts to restore Australian woodlands have emphasised stock removal, but this approach does not always lead to increased native species diversity. I examined the potential for the soil seed bank and the seed rain to provide propagules of native species in open and cleared woodlands under four grazing regimes in degraded white box woodlands in New South Wales during two seasons. The potential for smoke water to increase the germination rate of seeds was also examined. October and February samples differed significantly from each other, as did the interaction of season with clearing history, but two years of fencing had no effect on the seed bank or seed rain. No species were found in the seed bank or the seed rain that were not present in the standing vegetation. Smoke water increased germination of both natives and exotics. It appears unlikely that species lost from the system will recover without active reintroduction.

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David Hik must be thanked for his patience and tolerance of my foibles, especially near the end of this project when my distractions were many.

Dedication

For my grandparents, Calind and Annette Potts, and my parents, Robert and Judy Board.

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Chapter 1: Introduction

> ➢ The very earth itself is a granary and a seminary, so that to some minds its surface is regarded as the cuticle of one great living creature.
> -Henry David Thoreau (1883)

1. Introduction

The box woodlands of eastern Australia are one of the most endangered ecosystems in Australia. As much as 90% of the original woodlands have been cleared (Benson 1991) and the remaining patches are still being degraded (Goldney *et al.* 1995). Only 0.01% of white box (*Eucalyptus albens*) woodlands remain relatively unmodified (Prober & Thiele 1993a). There is increasing effort to restore degraded remnants to a more natural state, and most of the restoration efforts are focused on reducing or eliminating livestock grazing. However, stock reduction does not always lead to a return to a more natural state (e.g. Austin *et al.* 1981; Foran *et al.* 1982; Grice & Barchia 1995).

1.1. White Box Woodlands, Past and Present

Box woodlands once covered several million hectares from Queensland to Victoria along the western slopes of the eastern escarpment (Beadle 1981, Fig. 1.1). They existed as a mosaic of open woodland types on the undulating hills characteristic of this region (Fig. 1.2). John Oxley (1820), the first European explorer of the region in 1817, noted the grassy understory: "low forested hills gradually rising from the horizontal level… which

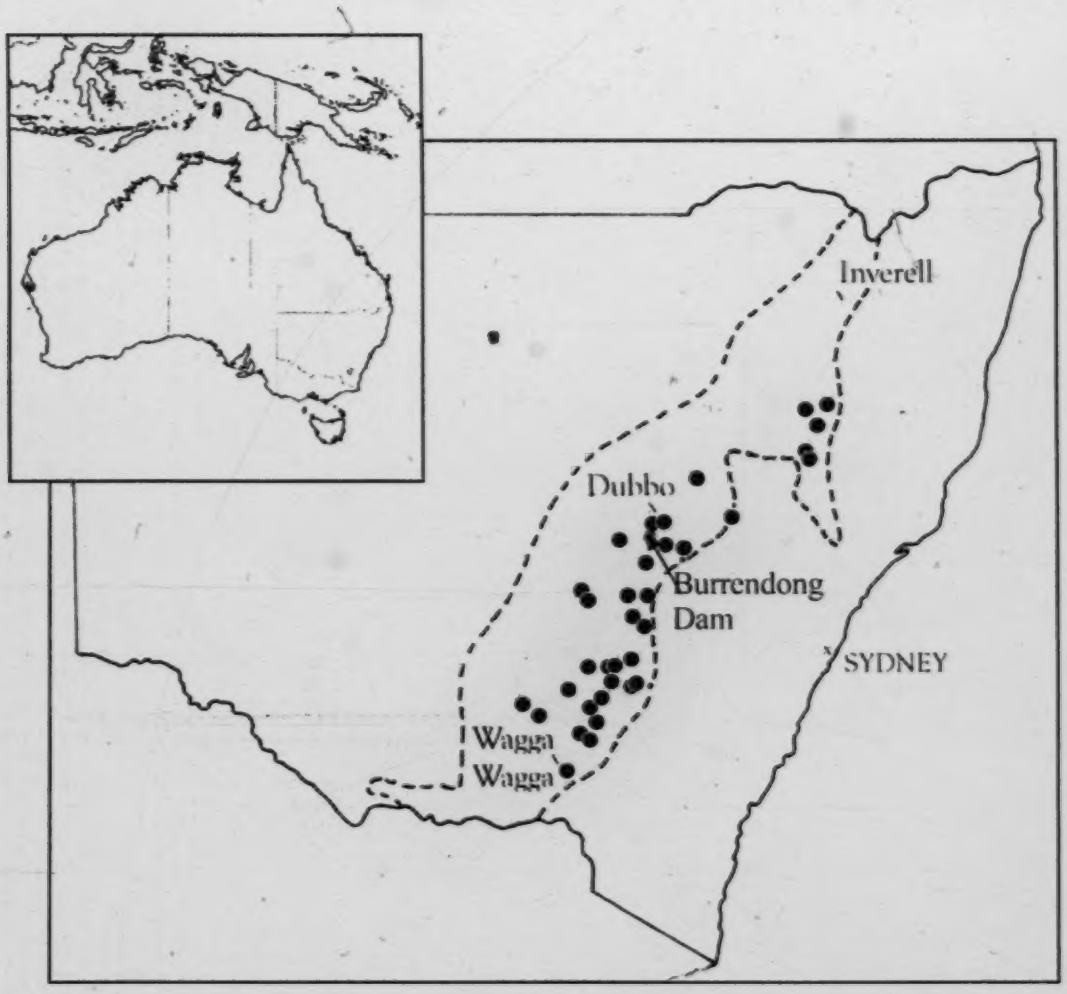

Figure 1.1 Map showing historic extent of white box woodland, location of remaining remnants and the Burrendong Dam study site (based on Prober et al. 2001).

were covered with excellent grass to their very summits and well calculated to afford an ample range of sheep pasture". Charles Sturt (1833), another early explorer of the region, gave the following description of the vegetation of the Macquarie River. "Upon these low grounds the blue gum trees were of lofty, but on the upper levels box prevailed".

Figure. 1.2. An early water color by Augustus Earle of the Wellington Valley New South Wales from 1826 looking east from government house. Note clearing has already begun in the valleys although the hills remain wooded. (S.H. Ervin Gallery, 1988; Discerning Eye, RNK Collection, NLA 1992. http://nla.gov.au/nla.pic-an2818294)

Two white box woodland community types are believed to have existed within this landscape. Shrubby white box woodlands had an understory of dense shrubs and a very sparse ground cover of forbs. This community type occurred on the steeper slopes and rockier soils (Croft *et al.* 1997). Oxley (1820) described this community in the following way: "… even the rocky hills … being covered with shrubs and grass intermingled among the box and small gum trees…." Grassy white box woodlands had an understory of very few shrubs and a ground-cover primarily made up of grasses and forbs. This community type is believed to have existed on deeper more fertile soils (Prober 1996), and was the focus of my study.

The original grassy white box community is believed to have been open woodland of widely spaced trees, with a density of about 30 large trees per hectare (Benson &

Redpath 1997). Oxley (1820) described the area around the Cudgegong River as "low irregular country … thinly covered with trees and grass". Early explorers and naturalists of the region reported that the general aspect was park-like (Andrews 1920). The understory was dominated by *Themeda australis*, kangaroo grass, and *Poa sieberiana* , grey tussock grass, (Moore 1959; Moore 1970; McIntyre and Lavorel 1994; Prober 1996). Other grasses, such as *Danthonia* spp., wallaby grasses , *Stipa* spp., wire grasses, and *Bothriochloa macra*, red leg grass, were present to various degrees but the specifics of their extent and distribution are unknown (Lodge 1984). The herbs that existed in this original community are undescribed but are believed to be similar to those found currently in cemetery remnants (Prober and Thiele 1995).

This region was the earliest inland area settled by Europeans with the towns of Bathurst established in 1813 and Wellington in 1823 (Clarke 1993). Changes to the woodlands due to livestock grazing, clearing and decreased fire frequency rapidly followed. Invasion by annual exotic grasses (*Briza minor*, *Bromus* spp., *Vulpia* spp., and *Horduem* spp.) was evident as early as 1878 (Bentham 1878). Because temperate woodlands tended to occur on better quality soils, most of the woodlands were rapidly cleared for cropping or modified by livestock grazing leaving a patchwork of remnants (Specht 1981; Bowie & Goldney 1987; Benson 1991; Lunt 1991; Prober & Thiele 1993a; 1995; McDougall & Kirkpatrick 1994).

Remnants subject to grazing, which includes all remnants except cemeteries and rail easements (Groves 1965, 1979; Tothill 1969; Groves *et al.* 1973; Stuwe & Parsons 1977; Lodge *et al.* 1984; Lunt 1991; Scarlett *et al.* 1992; Sivertsen 1993; Prober & Brown 1994; Prober & Theile 1993a, 1993b, 1995; Prober 1996), are believed to have

gone through a predictable series of species replacement by the dominant grasses (Moore 1953a, 1953b; Moore 1959, 1970; Whalley *et al.* 1978; Lodge & Whalley 1989; Prober & Theile 1995). These dominant species shifted from warm season perennials, such as *T. australis* and *P. sieberiana*, through cool season perennials and grazing tolerant warm season perennials such as *Danthonia* spp., *Stipa* spp., and *Aristida ramosa*, to predominantly annual exotic grasses such as *Vulpia* spp., annual fescues, *Bromus molliformis*, soft chess and *Aira caryophylla,* hair grass, as grazing increased. Changes in the subdominant grasses and forbs are less well documented but an increase of cool season annuals is consistent with studies in other areas (Whalley *et al.* 1978; Lodge & Whalley 1989). European settlement and its associated clearing and stock brought a large invasion of non-native weeds (Groves & Burdon 1986; Goldney & Bowie 1990). At present, only traveling stock routes and cemetery remnants contain predominantly native species (Prober & Theile 1993b; Windsor *et al.* 2000).

As a result of European settlement, the woodlands presently exist as remnants of various sizes and quality (Prober & Thiele 1995). After an intensive search of the central and southwest slopes of New South Wales, Prober and Thiele (1993a) found only three small patches with both tree cover and a relatively unmodified understory. Uncleared woodland patches typically have an overstory of white box, a limited shrub layer consisting primarily of *Olearia elliptica,* sticky daisy-bush, and *Dodonea viscosa*, hop-bush, and a ground layer dominated by *B. macra* and other perennial grasses such as *Danthonia* spp. And *Stipa* spp. During dry years in the summer months *B. macra* can appear dominant, especially after the annual grasses have senesced. Occasional small patches of *P. sieberiana* and *T. australis* are still scattered across the landscape but are

never dominant. Exotic species, particularly annual forbs and grasses, can be abundant in years of high rainfall, often exceeding 30% of the vegetative cover. In cleared patches of grassy white box woodland (where the overstory has been removed) the ground layer is similar, but has a higher abundance of exotic species, especially exotic annual grasses such as *Vulpia myuros* and *V. bromoides*, annual fescues, and *Bromus molliformis*, soft chess. Clearing of remnant woodland is continuing (Sivertsen 1994; Benson 1999). Patches that are not shrinking are declining in quality due to grazing, altered fire regimes, invasion by exotic species and nutrient addition (Goldney & Bowie 1990; Goldney *et al.* 1993, 1995, 1997; Yates & Hobbs 1997; Sivertsen 2000; Sivertsen & Clarke 2000).

1.2. Interest in and Methods of Restoration

There is considerable interest in conservation and management of native vegetation in Australia because of its long-term value for agricultural production and its importance for the conservation of native species (Wells *et al.* 1984; Benson 1987, 1999; Campbell 1994; Yates & Hobbs 1997; Hitchmough *et al.* 1989; Hodgkins *et al.* 2000). The value of native vegetation for amelioration of dry land salinity is becoming well accepted by scientists, land managers and graziers (Land Water Resources Research Development Corporation 1993; Barlow 1998), and there are initiatives to raise awareness of other values such as animal habitat and sustainable productivity (Yates & Hobbs 1997; Elix & Lambert 1997). On both public and private land, efforts to preserve or restore remnant woodland are increasingly focused on techniques and incentives for fencing and de-stocking (Gilfedder & Kirkpatrick 1995; Department of Land and Water Conservation 1996; Barlow 1998; Elix & Lambert 1997; Anonymous 2000; Hodgkins *et al.* 2000; Charles Sturt University Press Release 2001). Ecological restoration is the

process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2002). Restoration attempts to return an ecosystem to its historic trajectory.

There are also incentive programs to encourage conservation and restoration of remnant bushland on private property. The most popular incentives are subsidies for stock fencing and tree planting (Buchanan 1989; Anonymous 1995; Department of Land and Water Conservation 1996; Binning & Young 1997; Elix & Lambert 1997; Lambert *et al.* 2000). LANDCARE, Saving the Bush and Natural Heritage Trust programs are funding the fencing of remnants (Benson 1999). The Department of Land and Water Conservation, NSW (February 1996) has stated that "provision for fencing ... is vital for vegetation conservation". Barlow (1999) views fencing as the most important management requirement for restoration of remnant woodlands. Landholders identified fencing subsidies as one of their greatest needs in their personal restoration efforts in surveys conducted by Gilfedder and Kirkpatrick (1995), Lambert (1998) and Hodgkins *et al.* (2000). Of the seventeen Interim Biogeographic Regionalisation of Australian Bioregions, ten list fencing as one of the priorities for vegetation protection and eight list fencing as the first priority (Benson 1999). Fencing is clearly the restoration method of choice.

1.2.1. Fencing as Restoration

Livestock grazing is the most conspicuous disturbance across all woodland types and one that is easily manipulated by land managers. Historically heavy grazing of popular box (*Eucalyptus populnea*) woodlands in central New South Wales has lead to the elimination of desirable grass species such as *Dicanthium sericeum*, Queensland blue

grass, and *T. australis* (Hodgkinson *et al.* 1980). Although grazing is better managed today than in the past, most vegetation remnants west of the Great Dividing Range have been affected by past and present stock grazing and this is likely to continue to be a problem (Benson 1999). Grazing has been shown to degrade remnants of white box woodlands and other woodland types (Moore 1970; Adamson & Fox 1982; Lunt 1991).

Prober and Thiele (1993a) found a positive correlation between size of white box woodlands and exotic species richness in grazed remnants but not in ungrazed remnants. The small (0.04 - 5.5 ha), little grazed remnants maintained the general character of the pre-European woodland understory, while grazing caused changes to the dominant species and caused losses of some of the original abundant species (Prober & Thiele 1993a). Livestock grazing in remnant White Box woodlands lead to weed invasion and a gradual shift in native species composition and diversity as grazing levels increased (Prober and Thiele 1993a). Livestock grazing has been determined to be incompatible with the maintenance of native species diversity in grassy white box woodlands (Prober & Thiele 1995).

However, it remains unclear whether the removal of livestock grazing alone will restore white box woodlands, or Australian woodlands in general (Hobbs 1989; Cluff & Semple 1994; Petit *et al.* 1995). Fencing or removal of grazers has been successful in some situations. Pettit and Froend (2001) found that after seven years of exclosure from stock, jarrah (*Eucalyptus marginata*) woodlands showed a substantial increase in perennial species and a trend for species composition of fenced remnants to resemble species composition of ungrazed remnants. Cluff and Semple (1994) have found similar results in grassy woodlands in south-eastern Australia after only two years of stock

exclusion. Grassy woodlands of the northern tablelands of New South Wales showed regeneration of native shrubs and trees but only in the least modified remnants (Curtis 1994).

In other studies however, there was no recovery of species after five to seven years of fencing (Foran *et al.* 1982; Hobbs 1989; Grice & Barchia 1995). In western New South Wales semi-arid grasslands, *Danthonia caespitosa* was unaffected by grazing but responsive to seasonal rainfall differences and there was no response in community composition (Austin *et al.* 1981). Salmon gum (*Eucalyptus salmonophloia*) woodlands have not shown a significant response in native diversity after 7 years of fencing despite and increase in cover (Yates & Hobbs 1997a). The reasons why cessation of grazing may not enhance restoration efforts likely depend on other disturbances that have occurred along with livestock grazing, including clearing, grazing by feral animals (rabbits, goats, and pigs) and kangaroos, and invasion by exotics.

1.2.2. Native and Feral Grazers

Once perennial grass populations collapsed in semi-arid woodlands of eastern Australia the persistent grazing pressure from uncontrolled non-domestic herbivores prevented rehabilitation (Hodgkinson & Cook 1994). Elimination of sheep (and presumably other stock) from the rangelands may do little in the long term towards improved management if populations of native and feral herbivores are not also managed (Freudenberger 1995). The impact of feral and native herbivores may retard recovery of perennial grasses in de-stocked paddocks (Grice & Barchia 1995).

Kangaroo numbers may be elevated compared to estimated historic populations (Hik & Newsome Unpublished) and even without the additional pressure of livestock

grazing may prevent a return to a more natural state. Several rare and endangered plants in Hattah-Kulkyne National Park, where stock had been removed at the park's inception, did not increase until grazing pressure from kangaroos was eliminated. The appearance of several species can be directly linked to reduction of kangaroo grazing pressure (Sluiter *et al.* 1997). Despite markedly different metabolism, kangaroos and livestock can have remarkably similar effects on vegetation. Freudenberger (1995) found little difference between sheep-only and kangaroo-only grazing at Lake Mere in western New South Wales. The functional responses of herbivory among kangaroos, sheep and rabbits are remarkably similar (Short 1985).

Feral animals, especially rabbits, have affected the grassland and woodland communities since their introduction to Australia. Rabbit grazing has been shown to reduce recruitment of many perennial woody species (Cochrane & McDonald 1966; Johnstone 1968; Crisp & Lange 1976; Crisp 1978; Lange & Graham 1983; Cooke 1987; Auld 1990). *Callitris columellaris*, white cypress pine, regenerated only when protected from both sheep and rabbit grazing and did not regenerate when protected from sheep only or when unprotected in south-western Queensland (Johnstone 1968). Sheep were excluded from a South Australian semi-arid shrubland for 36 years but little or no recruitment of trees and shrubs occurred because of browsing by rabbits (Hall *et al.* 1984). Revegetation efforts in *T. australis* grassland have been severely restricted by rabbit grazing of both planted seedlings and naturally recruited seedlings (Carr & Muir 1993). It is expected that rabbits would have a similar effect on temperate eucalypt woodlands (Yates *et al.* 2000).

Figure. 1.3. Photographs illustrating uncleared (left) and cleared (woodlands) at Burrendong dam, New South Wales.

1.2.3. Clearing

Clearing (Fig. 1.3) has a much greater effect than merely the removal of overstory trees. Clearing of popular box woodlands has been associated with increased availability of water and nitrogen (Tunstall *et al.* 1981). As a general rule, when over 80% of the landscape is cleared over 30% of biodiversity may be lost (Simberloff 1992). This loss increases over the long term due to competition with invasions of weeds and difficulties in dispersing to distant remnants (Benson 1999). Loss of native species has been almost complete in some cleared areas of box woodlands in the central west of New South Wales (Goldney & Bowie 1990). These losses may be reversible through restoration techniques such as fencing and tree planting, but understanding how clearing has changed the existing vegetation is needed to understand how cleared areas might respond to restoration efforts.

1.2.4. Recruitment and Seed Dynamics

A less obvious reason for the mixed success of fencing for restoration is that many plant species lack the possibility to re-establish after fencing. The maintenance of

a species in and its recruitment into a community depends on the longevity of the plants, the opportunity to produce viable seed, the viability of that seed in the soil, and the opportunity to germinate and establish (Williams 1971; O'Conner 1991). If a species becomes extirpated from the standing vegetation of a remnant it must re-establish from either the soil seed bank or seeds dispersing into the remnant from other nearby remnants. An adequate seed supply is critical for population maintenance or re-establishment (O'Conner 1991). O'Conner (1991) proposes that perennial grasses may be especially prone to local extinction, and in particular *Themeda triandra*, a close relative of *T. australis* (until recently they were considered the same species), is a species that is likely to disappear permanently from area of sustained grazing. Generally, where livestock grazing has been excluded, increases in abundance have been restricted to annual and perennial species that have seeds which disperse long distances and to woody perennial species that maintain persistent soil seed banks or resprout from vegetative material (Yates & Hobbs 1997). The restoration potential for a habitat depends on the seed dynamics (those parts of a plant's life cycle involved in the dispersal and germination of seeds) of its species (Fenner 1985; Chambers & MacMahon 1994).

1.3. Seed Dynamics

Seed dynamics are the portion of a plant life cycle that are involved in dispersal and germination (Fig. 1.4). Seed dynamics begin with seeds on the standing vegetation. Many factors affect the number of seeds produced by the standing vegetation including, resources available to the plant for reproduction, pollination, predation on flowers and pre-dispersal seed predation (Levin & Kerster 1974; Louda 1982; 1989; Fenner 1985).

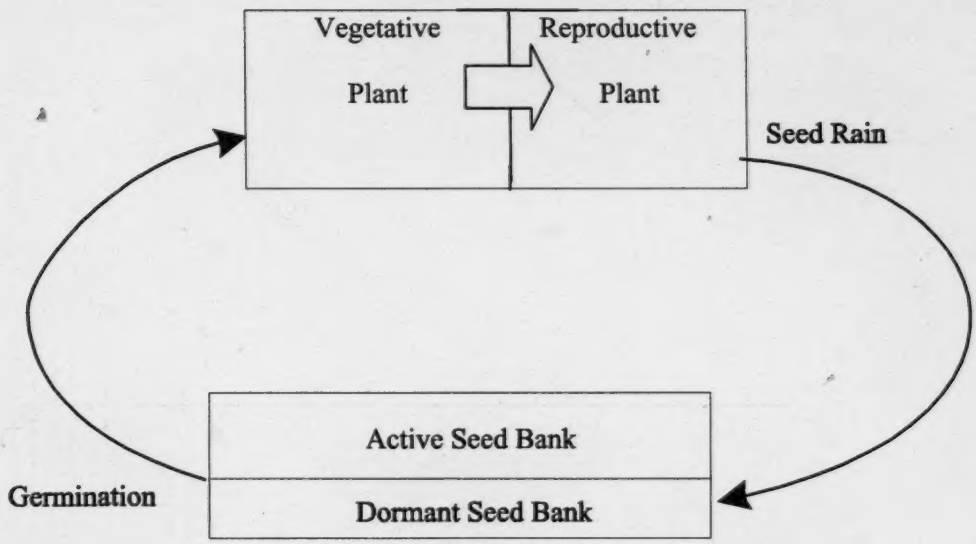

Figure 1.4. A simple model showing the general life cycle of plants.

The seeds then disperse via various mechanisms. Most seeds do not disperse far from their parent plant (Levin & Kerster 1974; Watkinson 1978; Rabinowitz & Rapp 1981; van der Pijl 1982; Fenner 1985; Carey & Watkins 1993; Chambers & MacMahon 1994; Cousens & Mortimer 1995), and this is especially true for grasses (Cheplick 1989). After dispersal seeds become part of the soil seed bank, which includes all viable seeds on or in the soil or associated litter (Thompson & Grime 1979; Simpson *et al.* 1989). Soil seed banks can be classified as transient, with seeds that remain in the soil for less one year; or persistent, with seeds that remain in the soil for more than one year (Simpson *et al.* 1989). Seeds can be lost from the seed bank through predation, deep burial, or loss of viability (Simpson *et al.* 1989). Seeds can also leave the seed bank through germination and enter the standing vegetation. Grazing can affect every aspect of this cycle.

1.3.1. Grazing and the Seed Bank

Grazing has little direct effect on the seed bank, although livestock can cause compaction of the soil which may reduce the rate of incorporation (Harper *et al.* 1965; Chambers & MacMahon 1994). It is also conceivable that grazing could alter the rate of seed loss due to decay by altering the nutrient balance in the soil. However, grazing does indirectly affect the seed bank through alteration of standing vegetation composition, seed production and seed rain. Numerous studies from around the world report reductions in the seed bank due to grazing. For example, the seed bank of Alberta prairies was reduced due to grazing (Johnston *et al.* 1969), and rabbit fencing increased the number of seeds in the seed bank of a mesic grassland in England (Edwards & Crawley 1999). Grazing also affects the species composition of the seed bank, often favouring annuals and eliminating perennial species. At Yathong, New South Wales, Leigh *et al* (1989) concluded that sustained grazing pressure by sheep, cattle, goats, kangaroos, and rabbits eliminated many of the "summer-green" perennial forbs and grasses and their soil seed bank. For example, *T. triandra* and *Heteropogon contortus* were eliminated from the established vegetation and the seed bank within 25 years of sustained livestock grazing in South Africa (O'Conner & Pickett 1992).

1.3.2. Grazing and the Seed Rain

While the seed bank may not be directly affected by grazing, the seed rain is very much affected by grazing. Grazers often act as dispersal agents for seeds (Agnew & Flux 1970; Bullock & Primack 1977; Schmida & Ellner 1983; O'Conner 1991; Chambers & MacMahon 1994). Grazing can alter the phenology of plants and thus affect when certain species are dispersed. In the semi-arid grasslands at Deniliquin, New South

Wales, grazing pressure on warm season perennial grasses, such as *Enteropogon acicularis,* was high in summer especially after rainfall events when growth was highest, and thus flowering was prohibited. Grazers can directly remove seeds and flower heads reducing the number of seeds in the seed rain. Sustained grazing during the growing season has commonly resulted in the near to total consumption of inflorescences of grasses thereby reducing seed production (Brown 1943; Tainton & Booysen 1964; Ambasht & Maurya 1970). Rabbits have preference for the floral parts of plants (Garson 1985; Leigh *et al.* 1987), particularly the seed heads (Myers & Poole 1963). In general, defoliation reduces seed production (Jameson 1963). Grazing can alter the resource allocation of plants towards reproduction and thus the numbers of seed in the seed rain (Paige & Whitham 1987). Grazing also reduced seed production of perennial grasses (Hodgkinson and Terpstra 1989). Grazing reduced seed production of *T. triandra, H. contortus* and *Botheriochloa insculpata* in South African grasslands by up to 78% (O'Conner & Pickett 1992).

1.4. Study Objectives

The primary objective of this study was to asses the impact of grazing (by livestock, rabbits and kangaroos) and clearing on the seed dynamics of white box woodlands and how this impact may vary among seasons. As reviewed above, grazing and clearing are the foci of rsestoration efforts in white box woodlands. How they influence the recruitment potential of native and exotic species will affect the success of restoration efforts in these communities.

I determined if species lost from the standing vegetation were capable of re-establishing from the seed bank or seed rain. A persistent seed bank may allow

population persistence after local extinction from the standing vegetation (Grubb 1977; Bakker *et al.* 1996; Bekker *et al.* 1997; Tilman 1997; Stocklin & Fischer 1999). Knowledge of which species are not represented in the seed bank can be just as important as knowing which species are represented (Fenner 1985). The increasing isolation of remnants should tend to reduce the probability of re-colonization from the seed rain (Fahrig & Merriam 1985; Menges 1990; Poschold *et al.* 1996). Native species that were of particular interest for white box woodlands restoration were examined for the potential contribution of sexual reproduction in their recovery. In particular, *T. australis* (the historically dominant understory grass), white box (the dominant overstory tree), and *B. macra* (the current dominant native grass) were chosen as focal species.

Stock grazing and woodland clearing have been associated with the invasion of previously wooded areas by exotic weeds (Lunt 1990; Humpheries *et al.* 1993). I also examined the predominance of exotic species in the seed bank and seed rain. Of particular interest were annual exotic grasses such as annual fescues. Many exotic weeds produce long term seed banks or readily disperse to new areas. If exotics dominate the seed dynamics of a remnant, then restoration techniques that increase recruitment from seed for all plant will favour exotic species solely because of numbers. This problem may be exacerbated by the tendency of exotics (primarily annuals) to produce more seed and for these seeds to persist in the soil for longer more readily than natives (primarily perennials) (Fenner 1985; Parker *et al.* 1989; Thompson *et al.* 1998).

Finally, I determined if germination rates of the seed in the seed bank, especially natives, could be improved when treated with water impregnated with smoke, as has been reported for other parts of Australia (Baxter *et al.* 1994; Dixon *et al.* 1995; Roche *et al.*

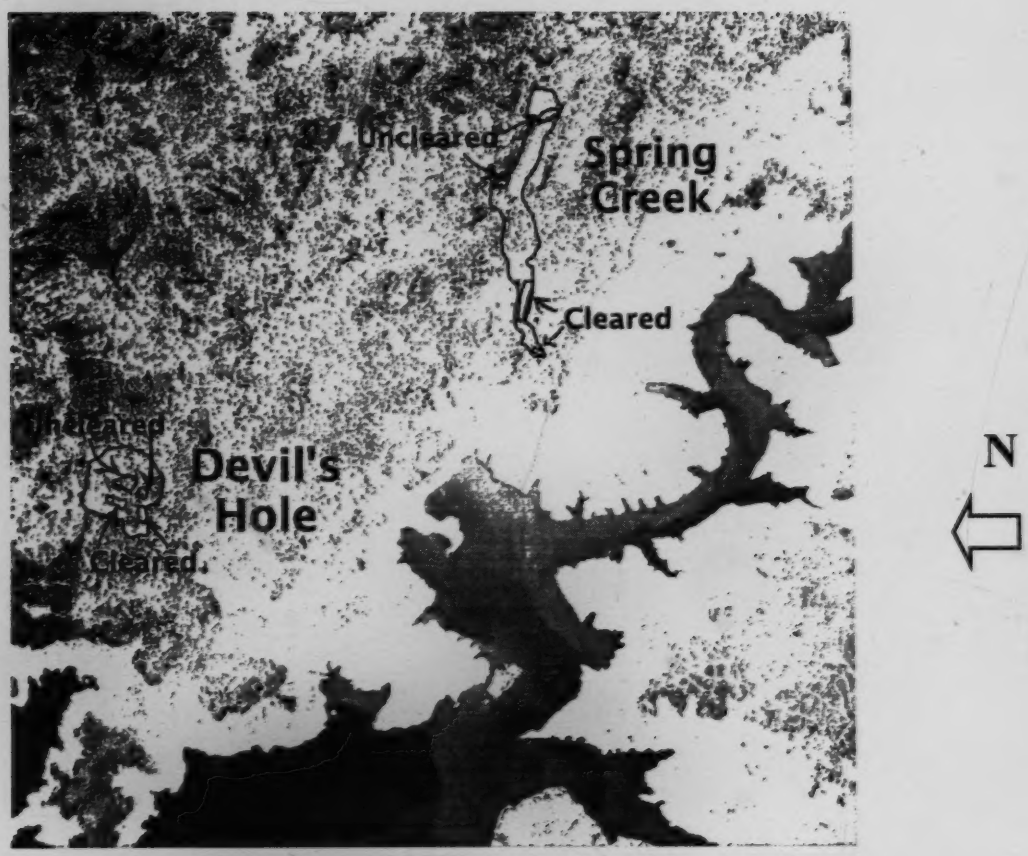

Figure 1.5. Aerial photograph of study area, showing blocks and locality distribution across the landscape.

1997; Read & Bellairs 1999; Askey-Doran *et al.* 2000; Reas *et al.* 2000; Tieu *et al.* 2001).

1.5. The Experiment

In 1997, CSIRO Division of Wildlife and Ecology (now Sustainable Ecosystems) established a long-term study at Burrendong Dam, New South Wales, to determine the effectiveness of fencing as a restoration tool in white box woodlands. As a part of this

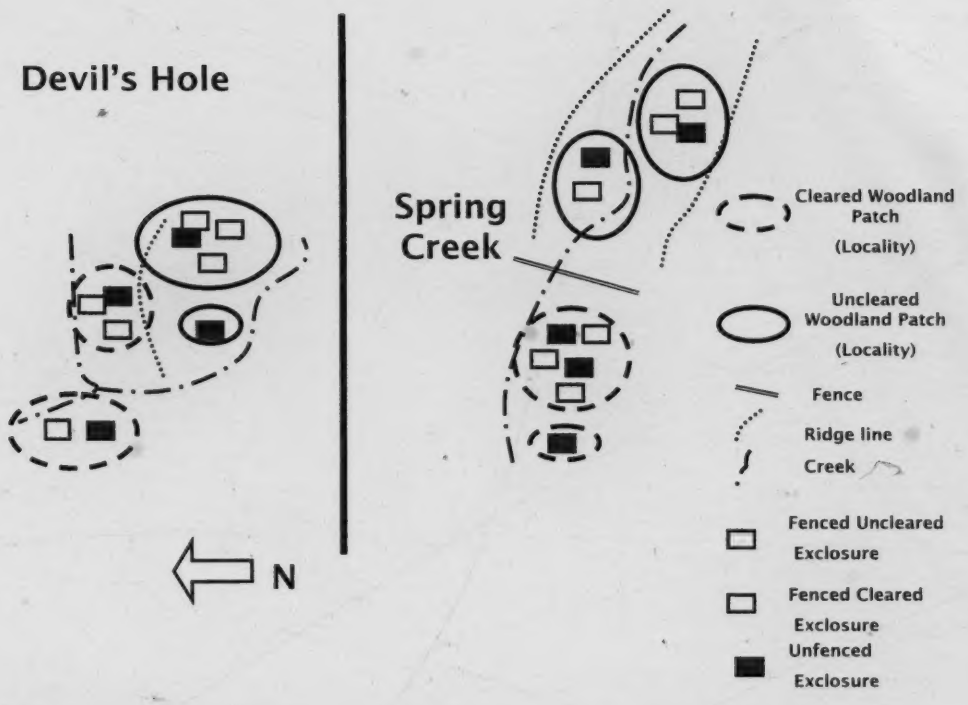

Figure 1.6. Schematic diagram of the arrangement of blocks (Devil's Hole and Spring Creek), localities and exclosures in the experiment.

study, I investigated the impact of grazing reduction and clearing on seed dynamics. The study is focussed on an experimental set of grazing exclosures established during summer of 1997 in cleared and uncleared woodlands. The experiment had an unbalanced split-split plot design. Two blocks, Spring Creek and Devil's Hole, were divided into two levels of degradation: cleared and uncleared (Fig. 1.5). Three experimental fence types were placed in each block and degradation level: rabbit, kangaroo and stock exclosure; kangaroo and stock exclosure; and stock only exclosure; each habitat/block combination was divided into two localities, based on the arrangements of the exclosures, in which a reference plot (unfenced plot) was placed. The localities were established to account for

some of the variation at the sub-site level (Fig 1.6). Exclosures and reference plots were sampled in spring and summer of 1999.

Each exclosure or reference plot (henceforth collectively referred to as exclosures unless specifically referring to a particular treatment type) measured 25m x 25m. The reference plots consisted of four steel fence posts, one at each corner of the exclosure. Stock fences consisted of a three to four strand plain wire stock fence about 1.5m tall. These effectively kept stock out but allowed access to both rabbits and kangaroos. Kangaroo fences consisted of wide meshed (25cm x 25cm) welded wire fencing about 2.5m tall. These fences effectively excluded both stock and kangaroos while allowing access by rabbits. The rabbit fences were 2.5m tall with wide meshed welded wire around the top 1m and a 1.5m skirt of chicken wire (rabbit fencing) around the bottom. These fences effectively excluded stock, kangaroos and rabbits. The seed bank and seed rain were sampled 2 years after the exclosures were established, during spring 1998 and summer 1999.

1.6. Summary

Grazing may impact soil seed bank dynamics in many ways. The direction of change is likely to depend on individual species characteristics although there may be functional groups that predict individual species response. However, the goal of restoration is to encourage native species and reduce exotic species. In particular, the dominant overstory and understory species must be capable of re-establishing in restoration areas. If these species are extirpated from the standing vegetation then they must be present in the seed bank or seed rain of the areas before they can re-establish. As well, species that are still present but at reduced numbers or cover will be limited to

vegetative spread if they are in limited numbers in the seed bank and seed rain. Exotic species will be difficult to eliminate or reduce if they dominate the seed bank and seed rain. Any restoration technique must therefore reduce the number of exotic seeds while increasing natives seeds in the seed bank and seed rain in order to be successful.

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Chapter 2: Seed Dynamics and Restoration of White Box Woodlands

> ➢ The consequence of all this activity of the animals and the elements in transporting seeds is that almost every part of the earths surface is filled with seeds…
> -H. D. Thoreau (1883)

2.1. Introduction

Box woodlands of eastern Australia are one of the most endangered ecosystems in Australia, with only about 10% of the original habitat remaining (Benson 1991). Despite interest in restoring and preserving woodland remnants (Hodgkins *et al.* 2000; Prober *et al.* 2001), many of these woodlands continue to decline, largely as a result of continued degradation from ongoing clearing and livestock grazing (Moore 1962; McIntyre & Lavorel 1994; Goldney *et al.* 1995; Sivertsen & Clarke 2000). A less obvious reason for widespread endangerment of these communities is that many native species lack the ability to re-establish viable populations, even under more suitable or restored conditions (Poschold *et al.* 1996; Allcock 2002a).

White box (*Eucalyptus albens*) woodlands occur in the inland region settled earliest by Europeans in the central western slopes of New South Wales. Because these temperate woodlands tended to occur on better quality soils, many areas were rapidly cleared for cropping or modified by livestock grazing (Bowie & Goldney 1987; Benson 1991; Prober & Thiele 1993, Prober *et al.* 2001). The original grassy white box community was characterised as an open woodland with 30 large trees per hectare (Benson & Redpath 1997), with an understory dominated by *Themeda australis* and *Poa sieberiana* (Moore 1959). Other grasses, such as *Danthonia* spp., *Stipa* spp., and

Bothriochloa macra were present to various degrees but the specifics of their extent and distribution are unknown (Lodge *et al.* 1984). The original forbs were not well described, but are believed to be similar to those found currently in cemetery remnants (Prober & Thiele 1995). Woodlands subjected to grazing are thought to have proceeded through a predictable series of dominant grasses (Moore 1953a; 1953b; Moore 1970; Lodge & Whalley 1989), shifting from warm season perennials such as *T. australis* and *P. sieberiana* to predominantly annual exotic grasses such as *Vulpia* spp., annual fescues, *Bromus molliformis* and *Aira caryophyllea* as grazing increased (see Allcock 2002a). Changes in the subsidiary grasses and forbs are less well documented, but an increase in cool season annuals is consistent with studies in other areas (Whalley *et al.* 1978; Lodge & Whalley 1989).

These woodlands now exist as remnants of various sizes and quality (Prober & Thiele 1995; Prober *et al.* 2001). The remnants consist of cleared and uncleared patches that still contain some native species from the original woodlands as well as many exotic weeds. During dry years, especially in the summer months, *B. macra* can appear to dominate especially after the annual grasses have died off. Occasional small patches of *P. sieberiana* and *T. australis* are still scattered across the landscape but are infrequently dominant. At the study site exotic species, particularly annual forbs and grasses, can be abundant in years of high rainfall often exceeding 30% of the vegetative cover (Allcock 2002a). In cleared patches of grassy white box woodland (where the overstory has been removed) the ground layer is similar, but has a higher abundance of exotic species, especially exotic annual grasses such as the annual fescues, *Vulpia myuros* and *V. bromoides*, and *Bromus molliformis*.

There is considerable interest in conservation and management of native woodland vegetation in Australia because of its long-term value for agricultural production and its importance for the conservation of native species (Benson 1999; Prober *et al.* 2001; Rokich *et al.* 2002). On both public and private land efforts to preserve or restore remnant woodland are increasingly focused on techniques and incentives for fencing and destocking (Gilfedder & Kirkpatrick 1995; Department of Land and Water Conservation 1996; Elix & Lambert 1998; Anonymous 2000; Hodgkins *et al.* 2000). However, it remains unclear whether the removal of livestock grazing will enhance restoration of white box or other Australian woodlands in general.

Removal of livestock grazing has produced inconsistent results in Australian woodlands with some areas responding well and others not at all. Pettit and Froend (2001) found that after seven years of exclosure from stock, jarrah (*Eucalyptus marginata*) woodlands showed a substantial increase in perennial species and a trend for species composition of fenced remnants to resemble the species composition of ungrazed remnants. Spooner *et al.* (2002) reported increased shrub and tree recruitment as well as increased perennial grass cover in response to fencing in Gray an Yellow Box woodlands in New South Wales In other studies there was no recovery of species after five to seven years of fencing (Foran *et al.* 1982; Grice & Barchia 1995).

The restoration of rare native species will depend on recruitment from a seed bank, seed rain, or assisted revegetation (e.g. Edwards & Crawley 1999; Rokich et al. 2002), and so the seed dynamics of a system needs to be assessed to determine whether *in situ* recovery of species is possible. Similarly, exotic species will be difficult to eliminate or reduce if they dominate the seed bank and seed rain. We evaluated the potential for

seed dynamics to contribute to the restoration of degraded white box woodlands with a long history of grazing in the central western slopes of New South Wales. Four different types of fencing were used to exclude successively smaller grazers (cattle and sheep, then kangaroos and then rabbits) in cleared and uncleared woodland patches. The soil seed bank and seed rain were sampled in spring and summer, and comparisons were made to the standing vegetation. Specifically, we assessed (1) whether the seed bank and seed rain contained native species, such as *T. australis* and *E. albens,* that had been more abundant prior to disturbance caused by historical clearing and grazing; (2) the extent to which the seed rain and seed bank might serve as a source of undesirable exotic species; (3) the influence of short-term fencing on seedbank dynamics; and (4) the overall role of the seed rain, seed bank and standing vegetation on restoration potential of white box woodlands.

2.2. Methods

2.2..1 Study Site

The study area was located on the foreshores of Lake Burrendong, a reservoir, on the Macquarie River, NSW (32° 40' S, 149° 6' W) on the western slopes of the Great Dividing Range of Australia. The climate is generally temperate, with warm summers (mean maximum 29-33° C) and cool winters (mean minimum 2-3° C). Annual rainfall was 666±29 mm yr^{-1} (mean±SE, 1951-1998 rainfall, Australian Bureau of Meteorology, Site No. 062003 - Mumbil), with considerable monthly variation but generally wetter winters.

The reservoir's foreshores were once dominated by white box woodlands, but the lower slopes were cleared of trees in the 1800's to promote pasture growth. Our study

focussed on patches of cleared and uncleared patches of grassy white box woodlands. Uncleared woodlands at Burrendong typically have an overstory of white box, a limited shrub layer consisting primarily of occasional sticky daisy-bush, *Olearia elliptica*, and hopbush, *Dodonea viscosa* and a ground layer dominated by perennial grasses including Wallaby grass (*Danthonia* spp.) and Spear grasses (*Stipa* spp.) with some *P. sieberiana* and *T. australis*. Exotic species, particularly annual forbs and grasses, may be abundant. In cleared patches of grassy white box woodland (where the overstory has been cleared), the ground layer is similar, but more highly invaded by exotic species, especially exotic annual grasses such as annual fescues (*Vulpia myuros* and *V. bromoides*) and Soft Chess (*Bromus molliformis*). *Bothriochloa macra* may dominate in dry years, particularly in summer after the annual grasses have died off (Allcock 2002a).

2.2.2. Experimental Design

The experiment utilized an unbalanced split plot design (*sensu* Snedcor & Cochran 1989). One block was placed in each of two small watersheds approximately 2 km apart. Eight patches of cleared and uncleared woodlands were identified (four per block; two cleared and two uncleared), and three types of exclosure fences plus reference, unfenced, areas (see below) were placed within each block/clearing level, for a total of sixteen areas, hereafter collectively referred to as exclosures, per block. Because each fence type was not present within each patch, at least one reference area was placed within each patch, plus one extra control in the largest patch, providing five additional reference areas (a total of 21 exclosures). The seed bank, seed rain and standing vegetation were sampled within each exclosure. Consequently there were three levels in which observations were grouped: (1) all observations were grouped within exclosures,

(2) exclosures were grouped within patches, and (3) patches were grouped within blocks. The fence effect was tested at the exclosure level, while the effect of clearing was tested at the patch level. Exclosures were sampled in the second year after the fences had been constructed, in October 1998 (spring) and February 1999 (summer). The difference between seasons was tested at the observation level.

Each exclosure measured 25 x 25 m. Reference plots were marked with four steel fence posts, one at each corner. The stock exclosure consisted of a 3 - 4 strand plain wire stock fence about 1.5 m tall, that effectively removed sheep and cattle, but allowed rabbits and kangaroos to enter the plot. The kangaroo exclosure consisted of wide mesh (25 x 25 cm) welded wire fencing about 2.5 m tall, and excluded both stock and kangaroos while allowing rabbits to enter. The rabbit fences were 2.5 m tall with wide meshed welded wire around the top 1m and 1.5 m of rabbit wire (chicken wire) around the bottom. A skirt of 0.5 m of rabbit wire was buried 20 cm below the surface of the ground perpendicular to the fence to prevent rabbits from digging into the exclosure.

2.2.3. Seed Bank Sampling

The soil seed bank was sampled by extracting 5 cm diameter by 5 cm deep soil cores, placed systematically to avoid other vegetation sampling areas within the exclosures. Edge effects were minimized by sampling at least 3 m from the edge of an exclosure. Nine cores were extracted from each exclosure in spring and 27 cores were collected from each exclosure in summer. Upon extraction, each core was placed in a plastic bag and air-dried at ambient temperature (25-30° C) for five days. Bags were sealed and stored at room temperature until April 1999 when they were processed in the greenhouse.

2.2.4. Greenhouse Germination Trial

In April 1999, nine cores from each sample period were combined and mixed, giving one mixture for the spring samples and three mixtures for the summer samples. These mixtures were subsequently divided into two equal samples. Each sample was spread into a germination tray (20 cm x 12 cm) containing 3 cm of a 50:50 mixture of steam-sterilized sand and steam-sterilized potting mix. The soil sample was lightly tamped to ensure good contact with the potting soil. Two sets of 5 trays of the sand and potting soil mixture (control trays) were established as well to help detect any contamination in the sand:soil mixture or seeds dispersing into the greenhouse. One tray from each pair (and 5 control trays) was sprayed with 5 ml of tap water. The second tray from each pair (and 5 control trays) was sprayed with 5 ml of a smoke-water solution consisting of 0.5 l of REGEN 2000® Direct, a commercially available aqueous smoke extract, added to 8.5 l of tap water. These 178 trays were placed randomly throughout a temperature-controlled greenhouse at CSIRO Sustainable Ecosystems in Gungahlin, ACT.

The greenhouse was maintained at an average daytime temperature of 25°C and an average nighttime temperature of 10°C. Trays were watered with a fine mist for two minutes, three times each day for the first two days, then twice daily for the next twelve days, and after that every other day until the end of the experiment. Trays were moved to a new random location in the greenhouse every two weeks, and each tray was monitored daily for new seedlings. When seedlings were old enough to be identified they were counted and removed from the trays. A representative sample of each species was grown until identification could be confirmed, or until 20 June 1999 when any remaining

unidentified seedlings were classified as unknown and the experiment ended. The number of seedlings per germination tray was converted to number of seedlings per m^2.

2.2.5. Seed Rain Sampling

Seeds were trapped using 10cm deep plastic cups (6 cm diameter: 28.2 cm^2) partially filled with an equal mixture of propylene glycol, water and alcohol, plus a small amount of detergent. Traps were set so that the lip of the cups were flush with the soil surface. The seed traps were placed systematically to avoid other sampling areas within the exclosures and at least 3 m from the edge of an exclosure. Nine seed traps were set in spring, and 27 seed traps were set in summer. Seed traps were opened for seven days, and then the traps were emptied into glass jars filled with 95% ethanol for storage until they could be identified. Seeds were identified, to species where possible, using a reference collection of seeds from the study area and descriptions and photographs in Friend (1983).

2.2.6. Analysis of Seed Bank and Seed Rain

Since a split plot design is inherently nested and the design ws unbalanced, the mixed procedure of SAS (SAS Institute 1999-2000) and associated procedures to test for model assumptions were used to fit a mixed linear effects model. A model fitting process similar to that outlined by Pinheiro and Bates (2000) was used to select the random effects models, which were then evaluated for deviation from the assumptions of mixed linear effect models.

Mixed linear effect models are generalizations of the standard general linear model that relax the assumption of independence between observations and allow for correlation between observations within defined groups (Pinheiro & Bates 2000). They

provided a powerful tool for analysis of grouped or hierarchical data exhibiting correlation within groups by allowing the covariance as well as the mean to be modeled. Mixed linear effects models contain both fixed and random effects, and the fixed effects were used to model the shift in mean due to given parameters. Random effects were used to model the variance and covariance within groups.

Our dependent variable in the basic model was the number of seedlings per germination tray or the log of the number of seeds per seed trap. The log transformation was used because of the non-normality of the data, which is typical of seed rain data (Rabinowitz & Rapp 1980). The fixed effects in the model were season of sampling (season), clearing status (clearing), and fence type (fence). The random effects were patch the sample was taken from (patch) and exclosure the sample was taken from (exclosure), and any appropriate interactions. The residual variance was modeled if the variance was not constant. The resulting models variables for the seed rain and seed bank are listed in Tables 2.2 and 2.3.

Residual plots for each grouping level including the observation level were used to check for homogenous variance. Scatter plots of each random effect were graphed against the other random effects to check for correlation, and quantile-quantile plots of residuals at each level were examined to test for normality. Finally, the type III sums of squares were used to construct Wald F values to test for the significance of the fixed effects (Milliken & Johnson 1984; SAS On-line Help, proc mixed 2000). The mixed effects models were used to evaluate only the total number of seeds per germination tray or seed trap. The number of native seeds and number of exotic seeds were not modelled because the assumptions of the model could not be met. The unbalanced design and large

number of samples without native or exotic seeds violated the assumptions of model and made model fitting difficult.

2.2.7. Analysis of Effects of Smoke Water on Germination

The smoked samples were tested for an increase in germination compared to unsmoked samples using a one-tailed paired t-test (Zar 1984). The normality of the differences between the smoked and unsmoked pairs was tested using the Kolmogrov and Smirnov goodness of fit test and visually checked for deviations from normality using normal probability plots. If they were not normal, a Sign test (Zar 1984) was used to test for a greater proportion of positive responses to smoke. The tests were repeated for only those species of native origin and again only for those species of exotic origin. The ratios of exotic to native species and annual to perennial species responding were compared using contingency table analysis. Native or exotic origin designation was based on Harden (1990-1993).

2.2.8. Comparison of Seed Rain, Seed Bank and Standing Vegetation

The seed bank, seed rain and standing vegetation were compared using rank order tables for each season. The descending rank of each species was calculated for each phase of the life cycle, ties were given the lowest rank. The species ranks were then placed into four categories based on their individual rank (1-10, 11-20, 21-30, and >30). Only species found in all three life phases were included in this analysis. The agreement between rank categories among the life phases was tested using the kappa statistics (Cohen 1960; SAS Institute 1999-2000). The kappa statistic is:

$$\hat{\kappa} = \frac{\sum \frac{\sum n_{ii}}{n_{..}} - \sum \frac{\sum n_{i.} \sum n_{.i}}{(n_{..})^2}}{1 - \sum \frac{\sum n_{i.} \sum n_{.i}}{(n_{..})^2}}$$

where n_{ij} is the cross tabulation of the frequency of the rank groups for the two of the life phases.

2.3. Results

2.3.1. Seed Bank Composition and Effects of Smoke Water

The total number of seedlings per germination tray was significantly greater in the smoked than unsmoked samples (Table 2.1). The removal of annual fescues (*Vulpia myuros* and *V. bromiodes*) from the analysis indicated that these species were masking the significant positive response of other exotic species to smoke water (Table 2.1). The annual fescues showed little response to smoke water. Native species also showed a significant, positive response to smoke water, with a mean increase of 14.1 seedlings compared to control trays.

Overall, the responses of individual species were generally positive, with 65 of 97 species having more seedlings on average in smoked trays than unsmoked trays. The response varied from increases of 20 seedlings per smoked tray for *Soliva stolonifera,* to 7 seedlings per unsmoked tray for *Geococcus pusillus* (see Table 2.5). The number of exotic or native species showing a positive response to smoke was proportional to the number of exotic or native species in the seed bank (total E:N=63:29, positive E:N=31:13, χ^2=0.1226, p=0.6961). The ratio of annuals compared to perennials

Table 2.1. Mean difference between the number of seedlings in smoked and unsmoked pairs of samples (±SE), the p-value of a one tailed t-test for an increase in germination in smoked samples (d.f. = 83), the number of paired samples with a greater number of seedlings in smoked than in unsmoked samples and the p-value of a one tailed sign test for a greater number of seedlings in smoked than unsmoked samples (n=84).

Species	Mean Difference (# of Seedlings)	t-Test: p-Value	Positive Responses	Sign Test: p-Value
All	29.3±16.9	0.0437	52	0.0188
All (without *Vulpia*)	60.7±12.2	<0.0001	59	0.0001
Exotic	1.48±17.5	0.4665	42	0.5434
Exotic (without *Vulpia*)	33.6±10.6	0.0011	52	0.0188
Vulpia only	-16.5±20.9	0.7955	29	0.9984
Native	14.1±4.16	0.0005	51	0.0315

responding to smoke was large compared to the ratio of annuals to perennials in the total seed bank (Total A:P =57:27, Positive A:P =38:7, χ^2=12.23, p=<0.001), and annuals also showed the largest numeric response (Table 2.5).

Importantly, no new species were recorded with the application of smoke water to enhance germination. In all subsequent analyses, I used the seed bank germination data from control (unsmoked) trays. Fire has been absent from the Burrendong system for at least 50 years, and using the slightly higher seed bank values associated with the application of smoke water in the greenhouse is not appropriate in the context of our assessment of seed dynamics in the field.

A total of 43,739 seedlings of 111 species were recorded. The average density across exclosure, patch and season was 58,900 seedlings/m^2, and exotic species had the greatest densities (49,100 seedlings/m^2, 54 species). Annual grasses accounted for over

Table 2.2. Marginal conditional F-tests for the fixed effects on the number of seedlings germinating per m^2 in the final model selected and the estimated random effects.

Source	Numerator Degrees of Freedom	Denominator Degrees of Freedom	Wald F-value	p-value
Intercept	1	60	116.2	<0.0001
Season	1	60	109.8	<0.0001
Clearing Type	1	6	5.90	0.0512
Fence Type	3	10	1.96	0.185
Season*Clearing	1	60	19.75	<0.0001

Standard Deviations		
Locality Level:	Exclosure Level:	Tray Level (σ^2 x $\lvert$Fitted Value$\rvert^{2\delta}$)
Intercept: 84.2	Intercept: 40.7	σ: 0.922
Season: 37.6		δ=0.840

half of the seedlings (31,900 seedlings/m^2, 9 species), and most of these were *Vulpia* spp. (22,600 seedlings/m^2). Native seedlings were relatively uncommon (4,940 seedlings/m^2, 41 species). Annuals dominated the seed bank (51,200 seedlings/m^2, 64 species) compared to perennials (2,350 seedlings/m^2, 32 species). Approximately 10% of total number of seedlings (4,890 seedlings and 16 'species') could not be identified. The most common of the unidentified seedlings was a dicotyledonous species, potentially *Hypochaeris glabra,* but identification was not conclusive (1,283 seedlings).

2.3.2. Effects of Season, Fencing and Clearing on the Seed Bank

The final model selected to test the fixed effects allowed the season effect to vary at the patch level and modeled tray level variance as $\sigma^2 \times |(\text{the fitted value})|^{2\delta}$ with σ estimated at 0.922 and δ estimated at 0.84 (Table 2.2). The modeling of the variance allowed for the increase in the variance as the estimate of the number seeds/m^2 increased. The grouping variable watershed was dropped from the final model because very little

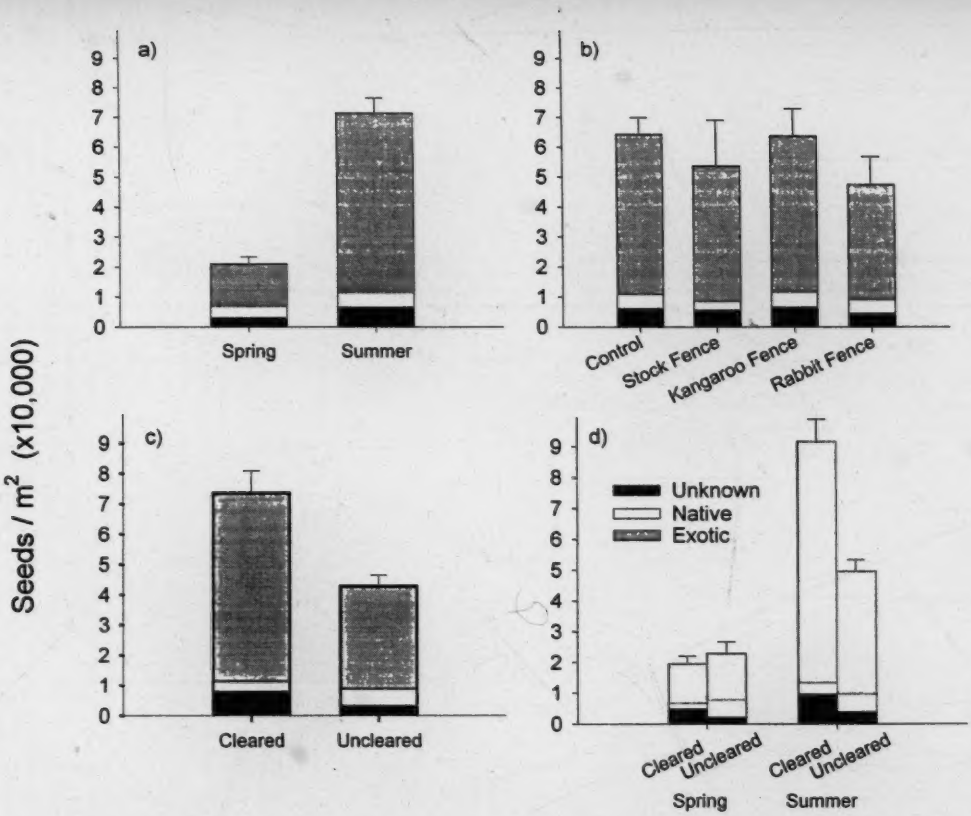

Figure 2.1. The number of seedlings per m^2 + SE divided into exotic, native and unknown by a) season of sampling, b) fence type, c) clearing and d) clearing and season.

variance was attributable to this level and the model fit was not greatly improved when this factor was included.

Not surprisingly, spring and summer samples differed significantly in the model (Table 2.2) with over three times as many seedlings germinated from summer samples as from spring samples (Fig. 2.1). This difference was largely due to exotic species, especially *Vulpia* spp. in summer (29,600 seedlings/m^2). Fence type was not significant in the model (Table 2.2), and there was very little difference between control, stock, kangaroo, and rabbit fences (Fig. 2.1b), although some species were more common inside or outside of the fences (see Table 2.5). For example, *Cerastium glomeratum* was 12 times more common in controls than in fenced exclosures, while *Stellaria media* was ten

times more common in fenced exclosures. Clearing alone was not significant in the model; however, its interaction with season was significant (Table 2.2). Cleared areas had on average 73,600 seedlings/m^2, compared to uncleared areas with 42,800 seedlings/m^2 (Fig. 2.1c). The apparent difference is attributable primarily to an increase in seedlings in the summer sample on the cleared patches.

2.3.3. Seed Rain Composition

A total of 10,170 seeds were captured in 367 seed traps (total area of 1.04 m^2) over both spring and summer sample periods (median number of seeds per trap = 13). Exotic seeds (N= 9,096) were found in 361 seed traps, while native seeds (N = 620) were found in only 112 seed traps. None of the species that once dominated the study site in the pre-settlement period (e.g. *E. albens* and *T. australis*) were found in the seed rain (see Table 2.5). Other perennial grasses were not abundant either, the most common being *Stipa scabra* with 43 seeds per m^2 during the spring sample. Instead, the seed rain was dominated by annual exotics. Of the top ten most abundant species in the seed rain (either spring or summer), only one was native, *Chenopopodium pumilio*, an annual. The most common species in the seed rain was the annual exotic grass, *Aira caryophyllea*, with an average of 2,200 seeds per m^2. Abundance of *A.caryophyllea* was highest in spring (3,840 seeds per m^2) compared to summer (149 seeds per m^2). The most abundant species in summer were the exotic annual fescues, *Vulpia* spp. although they were actually more abundant in spring (Table 2.5).

2.3.4. Effects of Season, Fencing and Clearing on the Seed Rain

The log of the mean number of seeds per trap in the spring sample was approximately half of the number recorded in the summer sample (Table 2.3, Fig 2.2).

Table 2.3. Test of fixed effects using marginal sums of squares and estimate of the random effects for the total seed rain (log of seeds per m^2 week).

Effect	Numerator Degrees of Freedom	Denominator Degrees of Freedom	Wald F-Value	P-Value
Season	1	341	15.12	<0.0001
Fencing	3	10	6.55	0.0254
Clearing	1	6	2.57	0.3693
Fencing*Season	3	341	2.72	0.0034
Clearing*Season	1	341	15.23	0.0002

Random Effects Estimates (Covariance Estimates):

Locality: 0.07742 Exclosure: 0 Residual: 0.911

The mean response for exotic species mirrored the overall seed number with the more seeds in spring than summer. The mean response for native species was the reverse of the pattern for the exotics, but the large number of traps that did not capture native seeds and the small number of natives seeds per trap when captured make this pattern difficult to interpret. The fence effect was significant for the log of the mean number of seeds per trap (Table 2.3).

The mean number of seeds in controls was large compared to other fence type (Fig. 2.2b). Exotic seeds showed a similar pattern. The mean response of native seeds declined as protection from herbivory increased however the response was small and the variation was comparatively large. The interaction of season with fence type was also significant (Table 2.3); however the pattern of the interaction was irregular. In spring, control and kangaroo fences had a significantly higher number of seeds than fenced exclosures in summer.

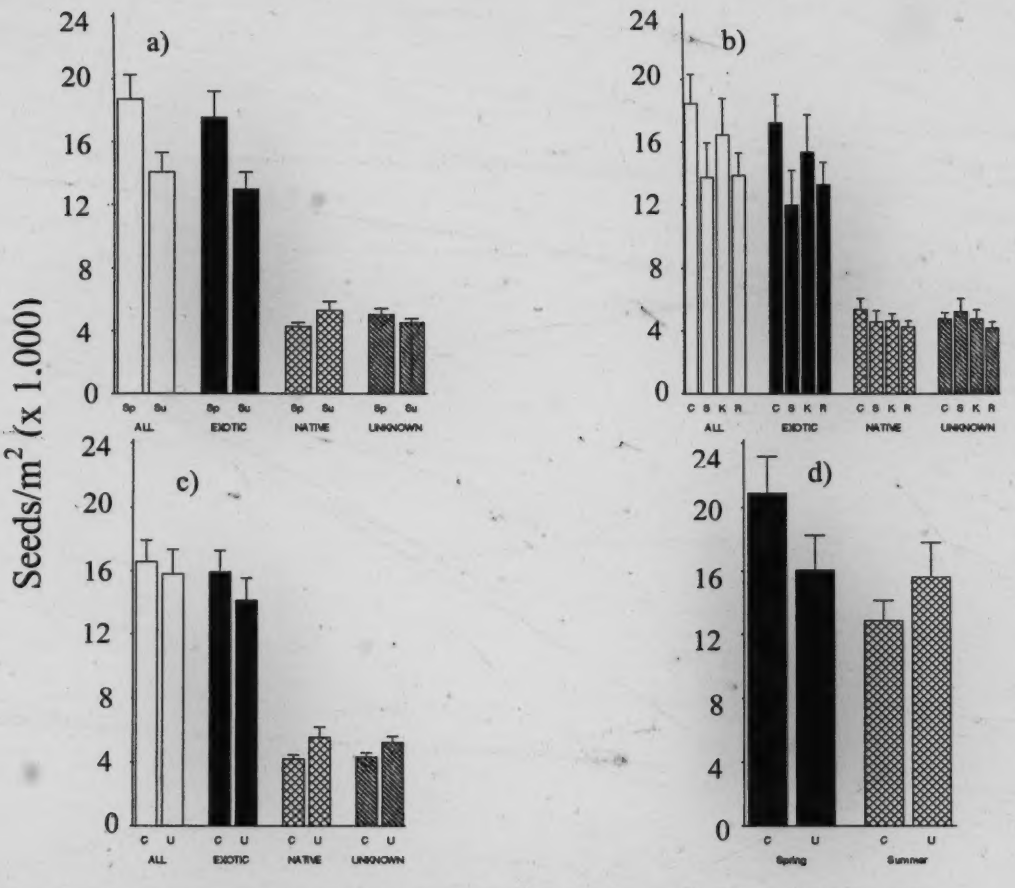

Figure 2.2. Mean number of seeds (error bars + SE) per m^2 categorized by all species, exotic species and native species in a) spring and summer, b) (C)ontrol, (S)tock,(K)angaroo, and (R)abbit exclosures abd c) by (C)leared and (U)ncleared localities and d) (C)leared and (U)ncleared by Season

The mean number of seeds per trap was not significantly different between cleared and uncleared areas but the interaction with season and clearing was significant (Table 2.3). Spring samples from cleared areas had significantly more seeds than summer samples from cleared area or samples from uncleared areas from either season. Exotic species showed a slightly higher mean number of seeds in traps with exotic species in cleared compared to uncleared areas, but the mean response of native species showed the reverse pattern with cleared areas having fewer native seeds trapped than uncleared areas (Fig 2.2c).

Table 2.4. Kappa statistic for the agreement of ranking of species and the associated p-value that agreement is zero, into the first three groups of ten (1-10, 11-20, 21-30) plus species ranked 31 or greater between life phases. Kappa values closer to 1 indicate greater agreement.

Season	Life Cycle Phase 1	Life cycle Phase 2	Kappa	One-sided p-value
Spring	Standing Vegetation	Seed Rain	0.0072	0.464
	Standing Vegetation	Seed Bank	0.0854	0.169
	Seed Bank	Seed Rain	0.0364	0.372
Summer	Standing Vegetation	Seed Rain	0.1402	0.070
	Standing Vegetation	Seed Bank	0.1165	0.201
	Seed Bank	Seed Rain	0.2692	0.002

2.3.5. Comparison of Standing Vegetation, Soil Seed Bank and Seed Rain

Excluding the unidentified 'species', the soil seed bank and seed rain were entirely subsets of the standing vegetation (Table 2.5). There were 233 species recorded in the standing vegetation compared to 111 in the seed bank and 57 in the seed rain. In the spring the seed rain, seed bank and standing vegetation were dominated by annual exotic species particularly the annual exotic grasses such as *Vulpia* spp. Only two native grazing tolerant perennials, *B. macra* and *Hydrocotyle laxiflora* (Prober & Thiele 1995), ranked in the top ten in spring for the any of the life stages and these were ranked 8th and 9th in the standing vegetation.

In summer, the native perennial grasses played a more prominent rule in the standing vegetation as the exotics died out and were not included in the vegetation cover estimates (Table 2.5). The seed rain and seed bank were still dominated by annual

exotics in summer, annual fescues were the most abundant species. The annual exotic forb, *Echium plantagineum*, dominated the summer standing vegetation. Overall, the seed rain, seed bank and standing vegetation did not agree on the rank categories of the species in the vegetation (Table 2.4). The most consistent ranking between the life phases was in the summer between the seed bank and the seed rain.

2.4. Discussion

The number of seeds in soil seedbanks varies greatly from 10^1 to 10^9 seeds/m^2 depending on the technique used to estimate the seeds density (per m^2), the habitat and season sampled. The average number of seeds (59,000/m^2) found in this experiment was high compared to studies using similar techniques in temperate Eucalyptus woodlands (30,000-36,000 seeds/m^2 (Carrol & Ashton 1965)). Bartolome (1979) reported 65,000 seeds/m^2 similar densities from an annual grassland in California dominated by *Vulpia myuros*. The seed bank at Barrendong was dominated by annual exotic grasses especially *Vulpia* spp. (a combination of *V. myuros* and *V. bromoides*). If *Vulpia* spp. seeds are not considered the number of seeds/m^2 (36,400 seedlings/m^2) are comparable with the values of Carrol and Ashton (1965).

The seed rain samples were also dominated by annual species especially exotic annual grasses. The overall number of seeds and the species composition of the seed bank and seed rain resemble the California annual exotic grasslands (as described by Bartolme 1979 and Evan 1975) more than the native Australian woodlands (Prober & Thiele 1993). These grassland types have become a permanent part of the California landscape (Heady 1977) and may have become a permanent part of the Australian landscape especially since the swamping of the seed pool by seeds of exotic species may

cause a permanent shift in species composition (Denslow 1985). Restoration of these habitats in California has been problematic (George et al. 1992) and is likely to be problematic in Australia.

2.4.1. Seasonality

Season had the largest effect on the soil seed bank and the seed rain. The soil seed bank summer sample contained over three times the seeds of the spring sample. Much of the season effect in seed bank numbers can be attributed to annual grasses such as *Vulpia* sp. and *Bromus molliformis* that germinate in autumn and winter and do not form a large persistent seed bank (Thompson *et al.* 1998). The seasonal variation of the seed dynamics found here is typical of annual grassland types in southern Europe where many of the annual grasses that dominate this system originate (Thompson & Grime 1979) as well as the exotic annual grasslands of California (Evans 1975; Bartolome 1979; Young *et al.* 1981; Hobbs & Mooney 1985). Thompson and Grime (1979) argued that this pattern was a result of grazing and seasonally predictable summer droughts. In our case, the season effect may be exaggerated by the fact that May 1998 was the start of an unusually high rainfall period following several years of below average rainfall. This is the typical rainfall pattern for the region (Bureau of Meteorology 1998) and the large drop in the number of seeds in the soil during periods of high rainfall may not be an unusual pattern for the region.

2.4.2. Effects of Herbivore Exclusion by Fencing

Short-term fencing did not influence the overall number of seeds in the seed bank, and this result is consistent with several other studies. For example, fields under different management regimes in the Netherlands had similar seed banks after eight years although

standing vegetation had begun to change (Bakker 1989), the seed banks of grazed fields and ungrazed roadsides did not differ in annual California grassland (Major & Pyott 1965), and Akinola *et al.* (1998) found no effect of simulated grazing on the soil seed bank of European limestone grassland topsoil during a six year microcosm study. The lack of a response may be because of a lag between reduction of grazing pressure and the response in the seed bank or because the variance in the seed bank could swamp out any changes in the seed bank in response to fencing.

There was however a significant interaction between season and fencing by seed rain. While the pattern of response to fencing and season is not consistent with the increasing level of protection with grazing the general pattern was for the spring samples and the summer control to be high and the protected exclosures in summer to be lower. This appears to be due to an abundance of seeds of exotic species in the summer control samples. This may be a result of more seed being produced over a longer period of time by the exotics as competition between plants is reduced by grazing.

The seed rain from outside the fence may have overwhelmed any effect of the fencing on the soil seed bank or seed rain. However a 3 m buffer along the edge of the fence was not sampled, and since most seeds do not travel more than 3 m from their parent plant (Levin & Kerster 1974; Rabinowitz & Rapp 1981; Verkaar *et al.* 1983; Poschold *et al.* 1998; reviewed in Harper 1977) the impact of seeds entering the seed bank from outside the fences should be low. Nevertheless, several studies have found long distance seed dispersal to be important (Kellman 1974; Hobbs & Atkins 1988; Beatty 1991; Hubbard & McPherson 1999; Nathan *et al.* 2002). These studies indicated

that at least for some species, increasing the size of the fence or remnant will not prevent the introduction of seed from outside of the area.

While the overall number of germinates did not respond to fencing, several species did respond. For example *Cerastium glomeratum* seedlings were more common in controls than in the fenced exclosures and were 24 times more prevalent in the control plots than in the stock fence. The responses of individual species tended to be associated with individual fences or habitat patches.

2.4.3. Clearing

Clearing by itself did not have a significant effect on seed dynamics, but the interaction with season was significant for both the seed bank and seed rain. This seems to be due to the larger number of exotic annual grass seeds in the cleared areas compared to the uncleared areas. The uncleared areas appear to be less invaded by these annual grasses and thus did not respond with as large an increase in seed stores in the summer. Annual grasses were less abundant in the seed bank in the spring sample, and the seed banks of these grasses are often reported to be very low in spring and autumn (Thompson & Grime 1979; Young *et al.* 1981; Hobbs & Mooney 1985; Morgan 1998).

2.4.4. Comparison of Seed Bank, Seed Rain and Standing Vegetation

The species in the soil seed bank and seed rain were a subset of the species in the vegetation. This indicated that new species were not dispersing from the surrounding vegetation and no remnant species from earlier conditions have remained in the seed bank. Hodgkinson *et al.* (1980) found the soil seed bank of *Eucalyptus populnea* woodlands contained no species of grasses or forbs not already present in the standing vegetation. The soil seed bank species of Victorian grasslands were also found to be

subsets of the standing vegetation (Lunt 1997; Morgan 1998). Similar to these studies, the seed bank at Burrendong contained a disproportionate number of annual exotic species when compared to the standing vegetation. The most abundant species in the seed bank and seed rain (*Vulpia* sp, *Bromus molliformis* and *Aira caryophyllea*) were primarily annual exotic grasses from the Mediterranean.

The seed bank at Burrendong is dominated by exotic, weedy species, and grazed grassy woodland communities where the understory was once dominated by perennial grasses may be especially prone to seed banks dominated by weeds. Seed bank studies often find a dominance of short-lived forbs and an absence of longer-lived species (e.g. Hodgkinson *et al.* 1980; Young *et al.* 1981; López-Mariño 2000), and an increase of annual grasses in temperate woodlands in Australia has been associated to the greater capacity of annual species to seed bank (Clarke 2000). In addition to the propensity of weedy species to produce seed banks, many of these species can maintain prolific seed production under heavy grazing and thus dominate the seed pool of grazed sites (Brown 1985). Even if native species are present in the seed bank they may have difficulty establishing themselves under competition from weeds (Curtis 1989; Allcock, in press).

2.4.5. Loss of Native Species

The vegetation at Burrendong lacks species believed to have been present in white box woodlands prior to European settlement. *T. australis* was likely the dominant understory plant (Moore 1953a; Moore 1970), but has not been found in the standing vegetation of the exclosures, although it has been located in a few small patches often in rocky outcrops. Many of the forb species expected to be present in the original white box woodlands (Prober & Thiele 1995) were not detected in the standing vegetation of the

exclosures and only a few were found in the study area. At the onset of this study, there was some hope that the missing species may have been hidden in the soil seed bank or dispersing into the site in the seed rain, but they were not found.

This is typical of the findings from other grassland and grassy woodlands particularly those areas with a long history of stock grazing disturbance. Species from these habitats, particularly the perennial grasses are not prominent in the soil seed banks and likely never form long-term persistent seed banks (Archibold 1981; Bekker *et al.* 1997; Bakker *et al.* 1996; McDonald *et al.* 1996; Lunt 1997; Bekker *et al.* 1998; Morgan 1998). Seeds of several common grassland species of Victoria many thought to have been present in White box woodlands appear to lack the ability to persist in the soil (McIntyre 1990; Willis & Groves 1991; Morgan 1995; Lunt 1995, 1996, 1997). Once species with short-lived seeds are lost from the standing vegetation it would have been only a few years before they are lost from the soil seed bank (McIntyre 1990; O'Connor 1991; Morgan 1995) since the number of viable seeds of any seed tends to decline exponentially with time (Fenner 1985).

Because of this, seed banks are rarely found to be a useful source of propagules for restoration particularly in grasslands and woodlands. Investigators from around the world in various habitats have concluded that the seed bank would not be source of the desired species in their restoration efforts. Williams (1984), Baker (1989), McDonald *et al.* (1996), Bekker *et al.* (1997), Akinola *et al.* (1998), and Bakker and Berendse (1999) came to this conclusion for grassland communities of Europe. Two of these studies suggested that even plants with persistent seed banks might be lost from the seed bank within a few years and that those plants with permanent seed banks, lasting more than 2-4

years, tended to be weeds or pioneer species not targeted for restoration (Williams 1984; Bakker 1989). Prins *et al.* (1998) estimated that only 8 to 51% of the target species were available for recruitment into restoration areas after 100 years of farming in Dutch grasslands. In Patagonia, *Festuca pallescens* (a native perennial bunchgrass) does not produce a large persistent seed bank and its seeds are rapidly lost, therefore it is difficult to restore from the soil seed bank (Bertiller & Coronato 1994). The soil seed bank of *T. australis* grasslands in Victoria, Australia was unlikely to be sources of propagules for restoration (Morgan 1998).

The seedling emergence technique used to quantify the seed bank in this study inherently underestimates the number of seeds and species in the soil seed bank because germination requirements of all seeds cannot be met (Major & Pyott 1965; Roberts 1981; Fenner 1985; Bigwood & Inouye 1988; Simpson 1989). When soil from this study was treated with the water-soluble portion of smoke there were significantly more seedlings, but no new species were detected. While the techniques used may not have detected all seeds present, the study does provide a strong indication of which species will most likely to respond to fencing and other passive restoration techniques. In general, these results suggest that the seed bank will not be a seed source for restoration at Burrendong or in other grassy woodlands with long histories of disturbance, even if other methods are adopted (e.g. Rokich et al. 200; Spooner et al. 2002). The seeds simply are not present.

When seeds required for restoration are neither in the standing vegetation nor in the soil seed bank they can be dispersed from elsewhere from either local or regional species pools (Zobel 1997; Zobel *et al.* 1998). Since white box woodlands are highly fragmented, the possibility of the seed rain to contribute significantly to the restoration is

very limited because most species have limited dispersal distance (Poschlod et al. 1996). The seed rain at Burrendong did not contain any of the missing species and was dominated by weedy exotics. In numerous studies throughout Europe the natural seed rain has also been dismissed as an ineffective source of propagules for restoration (e.g. Stampfli & Zeiter 1999; Bakker et al. 1996; Poschold 1996).

Clarke (2000) noted colonization of rehabilitated erosion gullies on the Northern Tablelands of New South Wales from surrounding grasslands is slow. *T. triandra* took 8 years to reappear after rest from grazing despite being abundant in adjacent vegetation, suggesting low levels of dispersal (Kennan 1969). Gaps in *Eucalyptus regnans* stands are not likely to regenerate if over 40 to 60 m wide (Cremer 1966). Those species with longer dispersal tend to be early successional species which are rarely targeted for restoration and are often classified as weeds (van der Pijl 1982). Those species that are reaching the remnants tend to already be present at the site or be weeds. Most remnants have lost a significant proportion of the native species, thus limiting their potential to recover through internal seed sources or through vegetative spread.

The loss of species from both the standing vegetation, soil seed bank and seed rain can lead to a permanent change in the vegetation. Once species have been lost or system parameters such as nutrients and soil conditions have been greatly altered, the system cannot return to its previous state just through removal of grazers or by other passive restoration techniques. This has been reported from several other systems. Seven years of cattle exclusion from an area of central Australian woodland gave no consistent trends in species composition over a seven-year period (Foran *et al.* 1982). Five years of exclosure from grazing in semi-arid woodlands of southeastern Australia

resulted in no restoration (Grice & Barchia 1995). Such persistent changes have been recorded for semi-arid woodlands in Australia and the South West and Great Basin areas of the United States (Leigh *et al.* 1989; Hodgkinson & Terpstra 1989; Hodgkinson & Cook 1995; Westoby *et al.* 1989) as well for some temperate woodlands (Yates & Hobbs 1997), and many other ecosystems (Booth 1941; Dublin *et al.* 1990, Hik *et al.* 1992; O'Connor 1991; Allen-Diaz & Bartolome 1997).

The two species that are believed to characterize white box woodlands, *E. albens* and *Themeda australis* appear to be particularly vulnerable to these problems. *T. australis* is estimated to have been lost from the standing vegetation of the Australian tropical savannas in the late nineteenth century (Shaw & Bisset 1955) and is likely to have been lost in most of the Burrendong area much earlier because of its longer history of settlement. In South Africa, *Themeda triandra*, a close relative of *Themeda australis*, is reported to recruit poorly from the seed rain (O'Conner 1991). In our study, *T. australis*, although producing seed in the small remnant populations in the study area was not detected in the seed rain. In addition past soil erosion may have eliminated seeds that were once present in seed bank. Seed from *E. albens* also does not travel far from the parent tree (Clayton-Greene & Ashton 1990). Seed production is periodic with a 2-3 year period between peak years (Clayton-Greene & Ashton 1990). The seed rain of *E. albens* is likely to be a source of propagules only in good years and even then only in a small area around parent trees. Aerial photographs of the Burrendong area show an increase in tree cover since 1960 concentrated around existing trees. However, no *E. albens* seed was detected in the seed rain of this study although one individual was found in the seed bank.

2.4.6. Restoration

For those species missing from the vegetation active seeding or planting will be needed to reintroduce them. Alternately methods to increase seed dispersal to the site may be investigated but these may lead to increases in dispersal of undesirable species as well. Careful selection of remnants for restoration will also be important (Prober *et al.* 2001). Choosing locations with an intact species composition and fewer weeds is an obvious step. As well, choosing sites near other more intact remnants may lead to greater success depending on connectivity and the overall species composition of the site, distance and the of seed flow between the two remnants and overall species composition.

The goal of restoration is not just the increase of desirable native species but also the reduction of undesirable exotic species. These species are typically r-selected and respond to the disturbance process that initiates the need for restoration. For example, *V. myuros* and *Hypochoeris glabra*, are both short lived species that produce abundant seeds. Both are reported to increase under grazing (Young et al. 1981; Bartolme 1979). For these species to decline in abundance the opportunity to establish needs to be reduced. Reduction in grazing may cause a rapid increase of undesirable species as they quickly invade and establish in patches created by grazing. Overtime these species may decrease in abundance as these open patches fill with preexisting vegetation. However, it may be possible for these species to occupy these patches not by living tissue but to fill these patches with litter and then re-establish themselves from with in this litter (Bergelson 1990; Brown & Rice 2000). Even if these species were extirpated from a remnant because of their ability to disperse larger distances present a constant threat for remnants as theses species can quickly occupy disturbance within restored or preserved

remnants (Hobbs & Atkins 1991). A similar strategy is employed by *Echium plantagineum* another problem weed. Although it does not disperse in space, it instead creates a long term dormant seed bank effectively dispersing in time and becoming along-term problem for restoration (Parsons & Cuthbertson 1992).

2.4.7. Smoke

The use of smoke water to increase germination is used and is being promoted as a restoration technique. However, since smoke water proportionately increased the germination of both native and exotic species it may not be as effective in white box woodlands or other communities with high numbers of exotics. This is especially true since there were many more exotic species in the seed bank than natives. If the objective is to restore perennial species or late successional species, smoke water application may be minimally effective since these species tend to respond less frequently. Unfortunately, seed banks in general are dominated by annuals and early successional species (Fig. 2.1, William 1984; Bakker 1989). As a final caveat, a species must be present in the seed bank to respond to smoke water. In less degraded white box woodlands smoke water or fire may be an effective tool in restoration since species capable of responding may be present in large enough numbers and weeds are not as common.

2.4.8. Conclusions

Despite the importance of seed dynamics for certain life history groups and for ecosystem processes, it is likely that seed dynamics will not be important in the conservation of species in late successional, closed habitats (Pickett & McDonnell 1989). These species generally do not form persistent seed banks (Brown & Oosterhuis 1981; Fenner 1985). Lunt (1997) found few species from remnant grasslands remained in

forest soils and concluded that restoration of grasslands species by implementing grassland management in the forests would not return the forests to grasslands. Morgan (1998) came to a similar conclusion about species-rich *T. australis* grasslands in Victoria. This study also found a weed dominated seed bank with a limited supply of species targeted for restoration. This implies that the soil seed bank will be more of a hindrance than a help for the restoration of white box woodlands given the woodlands original vegetation and historical use. Some form of weed management and a seed source for target species will have to be included in any restoration plan for these woodlands. This management could take the form of direct manipulation of site by spraying and seeding or by selectively choosing where restoration efforts are to be focused so that areas with the greatest potential are selected. At Burrendong several locations were found that still contain important native species in the standing vegetation. Management to encourage reproduction in these areas and recruitment into the surrounding area may provide the best alternative to more intensive management of the degraded location but will require a more thorough understanding of the early life history of these species and how the original grassy white box communities developed.

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Table 2.5. Species found in the exclosures, the family the belong to, their origin (Native, Exotic, Unknown after Harden 1990-1993), their life history ((A)nnual, (P)erennial, (P)erennial Bulb Forming, (B)iennial, (T)ree), the density of each species in the spring seed bank, treated with (S)moke or not (U), and seed rain, the density of each species in summer, treated with (S)moke or not (U), and seed rain and the rank (ties given the lower rank) order of the species in the standing vegetation in spring and summer.

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
Aira caryophylla	Poaceae	E	A	2630.01	2861.76	3838.06	5568.98	6711.52	149.7	13	
Amsinckia intermedia	Boraginaceae	E	A			3.74	16.17	25.15		74	
Anagallis arvensis	Primulaceae	E	A	511.99	1201.83	1.87	959.3	1871.9	304.4	9	
Arctotheca calendula	Asteraceae	E	A		5.39	9.36	3.59	19.76	7.49	140	
Arenaria serpyfolia	Caryophyllaceae	E	A	2673.13	2118.02	905.71	856.9	1158.71	89.82	34	
Argemone ochroleuca	Papaveraceae	E	A	10.78			14.37	8.98		147	50
Avena barbata	Poaceae	E	A							68	
Avena fatua	Poaceae	E	A				1.8	7.19		138	
Briza minor	Poaceae	E	A	258.69	323.36	479.06	1234.16	1194.64	22.46	32	
Bromus alopecuros	Poaceae	E	A							101	
Bromus brevis	Poaceae	E	A				8.98	14.37		82	
Bromus diandrus	Poaceae	E	A						1.25	37	
Bromus hordeaceus	Poaceae	E	A							127	
Bromus madrietensis	Poaceae	E	A							137	
Bromus molliformis	Poaceae	E	A	21.56	26.95	308.77	4255.78	4595.31	100.43	5	
Bromus rubens	Poaceae	E	A				34.13	14.37		22	
Carduus tenuiflorus	Asteraceae	E	B			44.91	195.81	215.57	9.98	10	33

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
Carthamus lanatus	Asteraceae	E	A	10.78		7.49	21.56	32.34	26.82	14	22
Centaurea melitensis	Asteraceae	E	A	48.5	86.23	114.15	750.91	765.29	64.87	8	
Centauria tenuior	Gentianaceae	E	A				8.98	10.78		60	26
Cerastium glomeratum	Caryophyllaceae	E	A	997.03	921.58		2236.57	2085.67		71	
Chondrilla juncea	Asteraceae	E	A							23	46
Cirsium vulgare	Asteraceae	E	B			16.84					
Cynodon dactylon	Poaceae	E	P							48	
Echium plantagineum	Boraginaceae	E	A	5.39	37.73	5.61	353.9	459.89	51.15	3	
Galium sp.	Rubiaceae	E	A				59.28	695.22	.62	18	56
Hedypnois rhagodioliodes	Asteraceae	E	A							46	
Heliotropium europaeum	Boraginaceae	E	A	37.73	32.34		14.37	14.37	1.87	147	
Hordeum leporinum	Poaceae	E	A			22.46	34.13	35.93	3.12	58	
Hypericum perforatum	Clusiaceae	E	P	269.47	528.16		747.32	815.59		35	4
Hypochaeris glabra	Asteraceae	E	A							4	56
Hypochaeris radicans	Asteraceae	E	P	161.68	452.71	2329.78	1650.93	1776.68	150.33		56
Juncus bufonus	Juncaceae	E	A	1913.23	1438.96	2419.6	1149.72	1413.8	201.48	51	
Kikxia elatine	Scrophulariaceae	E	A							105	8
Lactuca serriola	Asteraceae	E	B				1.8			128	
Lamium amplexicaule	lamiaceae	E	A							147	
Linum trigynum	Linaceae	E	A							52	
Lolium rigidum	Poaceae	E	A	16.17	5.39	1.87	273.06	215.57	26.82	21	
Marrubium vulgare	Lamiaceae	E	P	5.39	5.39		28.74	12.58		30	

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
Modiola caroliniana	Malvaceae	E	A				1.8				
Opuntia stricta	Cactaceae	E	P							114	27
Parentucillia latifolia	Scrophulariaceae	E	A							130	
Petrorhagia nanteuilii	Caryophyllaceae	E	A	21.56	16.17		476.06	661.09		81	48
Poa pratensis	Poaceae	E	P							141	56
Polycarpon tetraphyllum	Caryophyllaceae	E	A	43.11	183.24		39.52	48.5		93	56
Romulea rosea	Iridaceae	E	P							136	
Rostraria cristata	Poaceae	E	A							89	
Schinus molle	Anacardiaceae	E	T				3.59	3.59			
Sherardia arvensis	Rubiaceae	E	A							29	
Silene gallica	Caryophyllaceae	E	A		59.28	1.87	1.8			76	
Silene nocturna	Caryophyllaceae	E	A							94	
Silybum marianum	Asteraceae	E	B					1.8		57	
Sisymbrium officianale	Brassicaceae	E	A							85	
Solanum nigrum	Solanaceae	E	A	5.39			3.59	14.37		144	56
Soliva stolonifera	Asteraceae	E	A					134.73			
Sonchus asper	Asteraceae	E	A	5.39			3.59	7.19		28	
Sonchus oleraceus	Asteraceae	E	A	26.95	26.95	20.58	102.4	109.58	6.86	42	
Stachys arvensis	Lamiaceae	E	A	16.17	26.95		86.23	111.38		59	
Stellaria media	Caryophyllaceae	E	A	1805.44	1940.17	63.62	2153.94	1688.66	15.59	79	
Tolpis umbellata	Asteraceae	E	A							49	
Unknown	Asteraceae	E	B	1907.84	3389.92	129.12	4985.13	6716.91	82.34	157	
Verbascum virgatum	Scrophulariaceae	E	B	10.78	16.17			1.8		77	35
Verbena bonariensis	Verbenaceae	E	A	5.39			3.59	7.19		153	

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
Acaena echinata	Rosaceae	N	B							147	
Ajuga australis	Lamiaceae	N	P				3.59	5.39			
Alternanthera nana	Amaranthecaceae	N	A							126	
Aphanes arvensis	Rosaceae	N	A	528.16	571.27		564.08	571.27		92	41
Aristida ramosa	Poaceae	N	P							55	5
Aristida vagans	Poaceae	N	P							87	34
Arthropodium minus	Anthericaceae	N	P							66	
Asperula conferta	Rubiaceae	N	P	86.23	156.29		389.83	416.78		124	
Boerhavia dominii	Nyctaginaceae	N	A	237.13	614.39		177.85	213.78		114	
Bothriochloa macra	Poaceae	N	P		5.39		21.56	28.74	3.12	6	1
Bulbine bulbosa	Asphodelaceae	N	P	5.39			1.8			88	
Carex breviculmis	Cyperaceae	N	P							103	
Carex inversa	Cyperaceae	N	P							56	10
Chamaecyce drummondii	Euphorbiaceae	N	P							122	
Cheilanthes austrotenuifolia	Sinopteridaceae	N	P	10.78			14.37	7.19		26	12
Cheilanthes distans	Sinopteridaceae	N	P							114	
Chenopodium pumilio	Chenopodiaceae	N	A	625.17	485.04		271.26	240.72	1.25		
Chloris truncata	Poaceae	N	P			1.87				50	9
Cotula australis	Asteraceae	N	A	312.58	414.98		43.11	213.78	1.25	131	
Crassula sieberiana	Crassulaceae	N	A	1174.88	2743.19		1052.72	1530.57		113	
Cymbonotus lawsonianus	Asteraceae	N	P	5.39	32.34		46.71	39.52		43	
Daucus glochidiatus	Apiaceae	N	A	32.34	16.17	5.61	366.47	391.62	49.9	15	
Desmodium varians	Fabaceae	N	P				3.59			41	20
Dianella spp.	Phormiaceae	N	P							124	

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
Dichanthium serecium	Poaceae	N	P							109	
Dichelachne micrantha	Poaceae	N	P					3.59		62	51
Dichondra repens	Convolvulaceae	N	P	37.73	26.95		141.92	156.29		16	7
Dichopogon fimbriatus	Anthericaceae	N	P		5.39					19	
Digitaria brownii	Poaceae	N	P	5.39	10.78		1.8	25.15		67	
Digitaria divaricatissima	Poaceae	N	P								29
Elymus scaber	Poaceae	N	P	53.89	5.39		431.15	452.7	9.98	20	21
Enneapogon gracilis	Poaceae	N	P							153	
Enteropogon acicularis	Poaceae	N	P							44	36
Epilobium billardierianum	Onagraceae	N	P							157	
Eragrostis parviflora	Poaceae	N	P							138	
Eucalyptus albens	Myrtaceae	N	T			3.74		1.8	0.62		
Eulalia aurea	Poaceae	N	P							61	
Geococcus pusillus	Brassicaceae	N	A	5.39			44.91	21.56			
Glycine clandestina	Fabaceae	N	P							144	27
Glycine tabacina	Fabaceae	N	P			28.07		1.8	2.5	27	
Gnaphalium sphaericum	Asteraceae	N	A	183.24	199.41		152.7	237.13		75	51
Goodenia pinnatifida	Goodeniaceae	N	A							36	
Hibbertia obtusifolia	Dilleniaceae	N	P							96	
Hydrocotyle laxiflora	Apiaceae	N	P				3.59	12.58		7	45
Hypericum	Clusiaceae	N	P							109	23

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
gramineum											
Isoetopsis graminifolia	Asteraceae	N	A					5.39			
Juncus flavidus	Juncaceae	N	P							114	51
Juncus homalocaulis	Juncaceae	N	P							109	
Juncus subsedundus	Juncaceae	N	P							95	
Lepidosperma laterale	Cyperaceae	N	P								
Lomandra filliformis	Lomandraceae	N	P							123	
Lomandra multiflora	Lomandraceae	N	P							24	13
Luzula densiflora	Juncaceae	N	P							146	
Maireana enchylaeinoides	Chenopodiaceae	N	P							134	
Microlaena stipoides	Poaceae	N	P							53	15
Microtis unifolia	Orchidaceae	N	P							70	
Mysotis australis	Boraginaceae	N	A							132	
Ophioglossum lusitanicum	Ophioglossaceae	N	A				14.37	1.8		135	
Panicum effusum	Poaceae	N	P	10.78	134.73		17.96	64.67	0.62	80	14
Parietaria debilis	Urticaceae	N	A							157	
Paspalidium constrictum	Poaceae	N	P							151	
Paspalidium gracilis	Poaceae	N	P							114	37
Pimelia curviflora	Thymelaeaceae	N	P							143	
Plantago dubium	Plantaginaceae	N	P	64.67	59.28		8.98	30.54		129	51
Plantago turrifera	Plantaginaceae	N	A							102	
Poa seiberiana	Poaceae	N	P							72	16
Ranunculus	Ranunculaceae	N	A	285.64	414.98	3.74	379.05	574.86	18.71	121	

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
sessiflorus											
Rumex brownii	Polygonaceae	N	P	10.78	5.39	3.74	201.2	215.57	3.74	17	48
Scutellaria humilis	Lamiaceae	N	P	253.3	134.73		100.6	84.43		99	19
Sebaea ovata	Gentianaceae	N	A							98	
Senecio hispidulus	Asteraceae	N	P							104	41
Senecio quadridentatus	Asteraceae	N	P		10.78		7.19	5.39		84	39
Senna barclayana	Fabaceae	N	P							90	
Shoenus apogon	Cyperaceae	N	A							114	
Sida corrugata	Malvaceae	N	P						4.37	47	30
Siggesbeckia australiensis	Asteraceae	N	A							90	
Solenogyne belloides	Asteraceae	N	P				19.76	1.8		39	40
Solenogyne dominii	Asteraceae	N	P								
Sporobolus creber	Poaceae	N	P							54	41
Stuartina muelleri	Asteraceae	N	A	5.39	21.56		17.96	26.95		108	
Swainsona galegifolia	Fabaceae	N	P							31	6
Tricoryne eliator	Anthericaceae	N	P							153	
Trigonella suavissima	Fabaceae	N	A							114	
Triptolodiscus pygmaeus	Asteraceae	N	A	86.23	21.56		273.06	465.28		40	
Unknown	Unknown	N	P	1907.84	3389.92	129.12	4985.13	6716.91	82.34	157	
Urtica incisa	Urticaceae	N	P	37.73	48.5		48.5	32.34		69	
Veronica plebia	Scrophulariaceae	N	P							97	
Vittadinia cuneata	Asteraceae	N	P							153	51
Vittadinia muelleri	Asteraceae	N	P						10.6	133	56

				Spring			Summer				
				Seed bank		Seed Rain	Seed Bank		Seed Rain		
Species	Family	Origin	Life History	U	S		U	S		Spring Rank	Summer Rank
Wurmbea biglandulosa	Colchicaceae	N	P	10.78	10.78		123.95	141.92		100	
Oxalis sp.	Oxalidaceae	U	U	641.34	533.55	7.49	680.85	483.24	4.37	65	32
Unknown	Unknown	U	U	1907.84	3389.92	129.12	4985.13	6716.91	82.34	157	

Chapter 3. Synthesis

> ➢ As time elapses and the resources from which our forests have been supplied fail, we too shall of necessity be more and more convinced of the significance of the seed.
> -Henry David Thoreau (1883)

3.1. General Conclusions

The potential for the natural seed bank and seed rain to contribute to the restoration of white box woodlands appears limited. The seed bank and seed rain were dominated by exotic species, native species were limited in abundance and the pre-settlement dominant overstory (*Eucalyptus albens*) and understory (*Themeda australis*) species were absent from the seed rain and only one, *E. albens*, was detected in the seed bank. The effect of fencing on the seed bank was equivocal (Table 2.1). However, the effect of fencing on the seed rain, while inconsistent in spring, was significant in fenced exclosures in summer, with fewer seed trapped within fenced exclosures (Fig. 2.2a). Cleared localities typically had both a larger seed bank and seed rain. Cleared localities in summer had a larger seed bank than uncleared localities while the uncleared areas were not significantly different (Fig 2.1d). The seed rain had the reverse pattern with the spring sample from cleared areas being larger than the summer sample and the uncleared area not being significantly different (Fig 2.2b). The effect of smoke water was to increase both native and exotic species, with the exception of annual fescues (Table 2.1).

3.2. Fencing

Grazing has been shown to affect the seed dynamics of plants in some studies (e.g. O'Conner & Pickett 1992; Bertiller 1996; Navie *et al.* 1996; Edwards & Crawley

1999), while others, like this study, have found no effect of grazing (e. g. Major & Poyt 1965; Kinucan & Smeins 1992). However, there is no doubt that grazing can alter the seed dynamics of a community. Some species are lost from the seed bank a short term, after being lost from the standing vegetation due to grazing pressure (Hodgkinson *et al.* 1980, O'Conner 1991; George *et al.* 1992). Most of the studies finding a response were based on pre-existing patterns of grazing, while studies finding no response tended to be from exclosure experiments. Release from grazing pressure does not always result in a return to the original state (Noy-Meir 1975; Walker *et al.* 1981; Westoby *et al* 1989).

Grazing disturbance in California has converted perennial grasslands to annual grasslands with similar species and dynamics to those found at Burrendong (Heady 1958). The standing vegetation in California annual grasslands continues to be dominated by annuals after grazing pressure is removed (Biswell & Graham 1956; Bartolome & Gemmill 1981). The seed banks of these systems have a rapid turnover with most of the seed produced and germinating in the current year (Young *et al.* 1981). Consequently, the seed bank closely resembles the above ground vegetation (Bartolome 1979). In grasslands, dispersal and regeneration limit diversity and the establishment of new species (Grubb 1977; Tilman 1997). Most grasses do not disperse long distance (Chambers & MacMahon 1994) and therefore, grassland seed dynamics do not respond quickly to grazing reduction since re-establishment from outside of a species from outside a patch is limited.

3.3. Exotics

The dominance of the seed bank and seed rain by exotics is not surprising since they dominate the standing vegetation as well (Table 2.5 and Fig. 2.1). The exotic

species in this system are primarily species that are annuals which typically produce an abundant seed crop (Biswell & Graham 1956; Young *et al.* 1981). The swamping of the seed pool by seeds of exotic species may cause a permanent shift in species composition (Denslow 1985). The seasonal variation of the seed rain found here, high in spring and decreasing in summer, is typical annual grassland types in southern Europe (Thompson & Grime 1979). Thompson and Grime (1979) argued that this pattern was a result of predictable summer droughts and grazing similar to the patterns we see at Burrendong. In the grasslands and open woodlands of California a similar pattern has developed (Evans *et al.* 1975: Bartolome 1979). These grassland types have become a permanent part of the California landscape (Heady 1977; Heywood 1989) and may become a permanent part of the Australian landscape.

Seed dynamic studies often report a dominance of short-lived forbs and an absence of longer-lived species (e.g. Hodgkinson *et al.* 1980; Young *et al.* 1981; López-Mariño 2000). An increase of annual grasses in temperate woodlands in Australia has been associated to the greater capacity of annual species to accumulate in the seed bank (Clarke 2000). In addition to the propensity of weedy species to produce large seed banks, many of these species can maintain prolific seed production under heavy grazing and thus dominate the seed pool of grazed sites (Brown 1985). Even if native species are present in the seed bank they may have difficulty establishing themselves under competition from weeds (Curtis 1989; Allcock, 2002).

Exotic seeds (excluding annual fescues) showed a numerically larger response to smoke water than the native species. Native species were not more likely to respond to smoke than exotic species. Restoration projects where weeds are prevalent will have to

contend with the potential for the weeds (exotic species) to respond as well or better than the target species (natives) following treatment with fire or the application of smoke water.

3.4. Species Loss

The standing vegetation at Burrendong currently lacks species believed to have been present in white box woodlands prior to European settlement. *Themeda australis* was likely the dominant understory plant (Moore 1953, Moore 1970), but has not been found in the standing vegetation of the exclosures or other vegetation monitoring plots (K. Allcock, unpublished data).

The loss of species from both the standing vegetation and the soil seed bank can lead to a permanent change in the vegetation. Once species have been lost or system parameters such as nutrients and soil conditions have been greatly altered, the community cannot return to its previous state just through removal of grazers or by other passive restoration techniques alone. This result has been reported from several other ecosystems. For example, seven years of cattle exclusion from an area of central Australian woodland gave no consistent trends in species composition (Foran *et al.* 1982). Five years of exclosure from grazing in semi-arid woodlands of southeastern Australia resulted in no restoration of native species (Grice & Barchia 1995). Such persistent changes have been recorded for semi-arid woodlands in Australia and the South West and Great Basin areas of the United States (Leigh *et al.* 1989; Hodgkinson & Terpstra 1989; Hodgkinson & Cook 1995; Westoby *et al.* 1989), as well for some temperate woodlands (Yates & Hobbs 1997) and many other ecosystems (Booth 1941; Dublin *et al.* 1990; Hik *et al.* 1992; O'Connor 1991; Allen-Diaz & Bartolome 1997).

3.5. Fragmentation

The potential for the seed rain to be useful in fragmented landscapes is inherently limited because most species have limited dispersal distance (Poschlod *et al.* 1996). Those species with longer dispersal tend to be early successional species which are rarely targeted for restoration and are often classified as weeds (van der Pijl 1982).

Seed rain has not been deemed effective in other studies assessing their potential to restore native species (Poschlod *et al.*1996). Seeds of true prairie grasses (i.e. big blue stem *Andropogon gerardi*) are not in seed rain and limit the recruitment of these grasses in to restoration areas (Rice *et al.* 1960). In numerous studies throughout Europe the natural seed rain has been dismissed as an ineffective source of propagules for restoration (e.g. Stampfli & Zeiter 1999; Bakker *et al.* 1996; Poschold 1996). In the tablelands area of New South Wales, colonization of erosion gullies from the surrounding grassland was slow (Davies 2000). In South Africa, *Themeda triandra* is reported to recruit poorly from the seed rain (O'Conner 1991). *T. australis*, although producing seed in the small remnant populations of the study area, was not detected in the seed rain.

Seed from *E. albens* does not travel far from the parent tree (Clayton-Greene & Ashton 1990). While seed production of *E. albens* is highest in the summer months (Curtis1989), it tends to be periodic with a 2-3 years between peak years (Calyton-Greene & Ashton 1990). Thus the seed rain of *E. albens* is likely to be a source of propagules only in these good years and even then only in a small area around parent trees. No *E. albens* seed was detected in the seed rain of this study although one individual was found in the seed bank.

3.6. Restoration

The seed rain and seed bank have rarely been useful source of propagules for restoration. Investigators from around the world in various habitats have concluded that the seed banks are not sources for the desired species in their restoration efforts those species with permanenet seed banks, lasting more than 2-4 years, tended to be weeds or pioneer species not targeted for restoration (Williams 1984; Baker *et al.* 1989; Bakker 1989; Akinola *et al.* 1998; McDonald *et al.* 1996; Bekker *et al.* 1997; Bakker and Berendse 1999). Prins *et al.* (1998) estimated that only 8 to 51% of the target species were available for recruitment into restoration areas after 100 years of farming in Dutch grasslands. In Patagonia, *Festuca pallescens* (a native perennial bunchgrass) does not produce a large persistent seed bank and its seeds are rapidly lost, therefore it is difficult to restore from the soil seed bank (Bertiller & Coronato 1994). The soil seed bank of *T. australis* grasslands in Victoria, Australia was unlikely to be a source of propagules for restoration (Morgan 1998). At Burrendong, few of the desired species were found in the seed bank and those that were present were in low numbers.

3.7. Limitations of the Burrendong Experiments

This study has several limitations to making strong inferences from it. First, the fences were only been in place for a short time period, two years prior to sampling, and therefore the seed bank may not yet have responded to fencing. Second, although seed travel only a short distance and those that do not appear capable of transport of extremely long distances, the size of the fences only 25m x 25m was limited and may have allowed a strong influence from outside the fence. Since seed banks have a natural large variation changes produced by grazing may be masked.

Third, the time for the greenhouse germination was limited to two months, and while new germinates failed to appear in most trays, a bias towards faster germinating species may exist. The difference between the spring and summer samples may also be, in part, due to differences in storage time. This was necessary, however, to standardize the greenhouse conditions. Fourth, germination is often dependent on numerous cues, and only standard greenhouse conditions and a smoke treatment were used. Consequently seeds requiring cold stratification or heating may have been missed in these trials.

Fifth, the seed rain was sampled only 2 times for a one week period in each season. This may limit the ability to detect all species or determine patterns of seed rain abundance. Treatment responses may also be masked by large natural variation in the seed rain.

3.8. Future Research

White box woodlands are especially dependent on restoration for preservation with only a few widely scattered sites of high quality. While three of these are sites known to have both over and understory intact and six other locations have a relatively intact understory, their preservation alone is unlikely to effectively in maintaining this habitat in the landscape (Prober & Thiele 1993; Thiele & Prober 2000). Efforts to readily identify those remnants that have the most potential for restoration are needed. In addition, the loss of species from the standing vegetation and seed bank, as well as the limited dispersal, will require active management for the establishment of native species. Research has been conducted to assess the effectiveness of establishment of *T. australis* in natural grassland habitats of Victoria (McDougall 1989; Morgan 1998). Expanding

this research to include white box woodlands would be worth pursuing. Research devoted to understanding how weeds and exotics can be controlled would also be useful. Research in other grassy woodland habitat indicate that while fire, a large component of the natural disturbance regime, has the potential to reduce weeds briefly it often increases weeds and must be used with caution (Davies 2000). White box woodlands are unlikely to respond to passive restoration efforts and will require active management, such as seeding, planting and weed management, to increase native species diversity and abundance. Research to identify effective techniques of active management is needed.

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